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THE FORESTS OF THE FLATHEAD VALLEY, MONTANA

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE OGDEN GRADUATE SCHOOL OF SCIENCE, IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

(DEPARTMENT OF BOTANY)

384436

BY
HARRY N. WHITFORD

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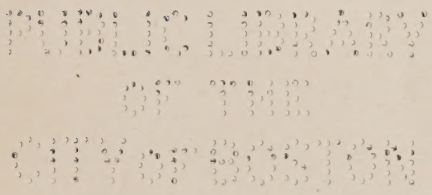

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THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

INTRODUCTION.

THE factors concerned in the grouping of plants are classified by SCHIMPER[2] as climatic and edaphic. When the climate of any region is such that a particular form of plant is favored, in most instances it gives character to the vegetation. For example, in the eastern United States the climate favors the tree form and gives rise to a "forest formation." If the grass form predominates, however, a "prairie formation" is the result. Again, if the climate be such that the cactus form gives the tone to the landscape, the "desert formation" is developed. Two such formations are shown in *fig. 1*, which is a view of a portion of the Flathead valley looking west from a high mountain. In the distance on the west side of the valley is a prairie formation; on the east side is a forest formation.

However, if one stands on a mountain top and looks down into these formations, he will observe that isolated areas in the forest do not contain trees, but may have a prairie, a swamp, a clearing, or a heath. The prairie formation may contain forests along streams or on protected hillsides. Also, in the forest formation there may be areas occupied almost exclusively by one, two, or more species of trees; while at a little distance there may be another area with entirely different trees. In other words, the composition of the forest changes from place to place. To distinguish these local groups from the general climatic grouping, SCHIMPER has called them "edaphic formations." By other authors they have been called "plant societies," "plant associations," or merely "plant forma-

[1] This paper is based on work as a collaborator in the U. S. Bureau of Forestry, to which acknowledgment is here made for permission to publish.

[2] SCHIMPER, A. F. W., Plant geography upon a physiological basis (translated by FISHER) 159–161. 1903.

FIG. 1.—View looking southwest from a high point in the Swan Mountains from just beyond the northeast limits of the map; Flathead Lake in the distance; the point of land extending into the lake is the delta of Flathead River; on the west side of the valley at the head of Flathead Lake a prairie formation; on the east in the foreground a forest formation. The edaphic areas shown in the forest formation are Ross Lake in the immediate foreground; north and south of this meadows; to the right Echo Lake; midway between Ross Lake and the delta is "nigger" prairie. In the prairie formation the course of Flathead River may be seen by the line of forests along its banks.—From photograph by ELROD.

tions."[3] *Fig. 1* will also illustrate these smaller groups. In the foreground may be seen a pond which contains its characteristic plants; to the right of this a meadow; and between the pond and Flathead Lake a local prairie. These are in the forest formation. While the soil factors determine primarily the variety of the plant landscape, other factors must be taken into consideration. In this paper, however, the convenient term "edaphic formation" will be used.

COWLES[4] was the first to show clearly that plant societies are not static, but dynamic. In brief, his contention is that the plant society changes with the physiographic changes that are constantly going on. In a former paper[5] I have attempted to correlate the various plant societies found in northern Michigan. In that study it is shown that the region lies in a deciduous forest formation, and that while the coniferous forest societies are present in the more xerophytic conditions, there is a tendency for them to be replaced by the climax society, the beech-maple combination. The present study, made in a region with a somewhat different climate, was undertaken to determine whether the various plant societies could be correlated in the same way. For this purpose a general survey was made of the Flathead valley, and a portion of it was selected to study in closer detail. No attempt was made to study the conditions in the higher altitudes where a different climate prevails.

PHYSIOGRAPHY.[6]

There exists a close relation between the development of the physiography of a region and the life history of its forest formation; hence the necessity of describing the topographic features of the Flathead valley. It is a well-defined physiographic unit, situated in the northwestern part of Montana, about long. 114° 30′ W. and lat. 47° 30′–49° N. (*fig. 2*). The altitude of the valley is approxi-

[3] For a discussion of the subject, see COWLES, H. C., The physiographic ecology of Chicago and vicinity. BOT. GAZETTE **31**:74–76. 1901.

[4] *Loc. cit.* pp. 75–108, 145–182.

[5] WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZETTE **31**:289–325. 1901.

[6] See ELROD, M. J., The physiography of the Flathead Lake region. University of Montana Bull. 17: 197–203.

mately 900^{m}, and it extends from the Canadian boundary about 160^{km}, a little to the east of south, to the low Jocko Mountains. A number of mountain ranges form its western border, and the front range of the Rocky Mountains with sub-ranges lie directly east, the

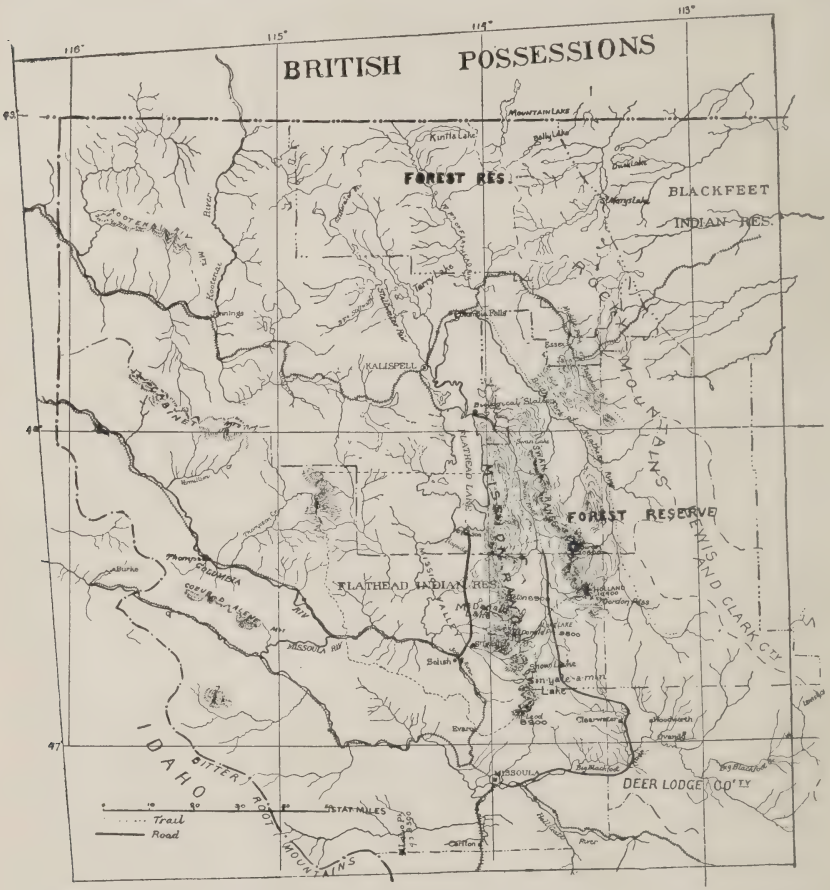
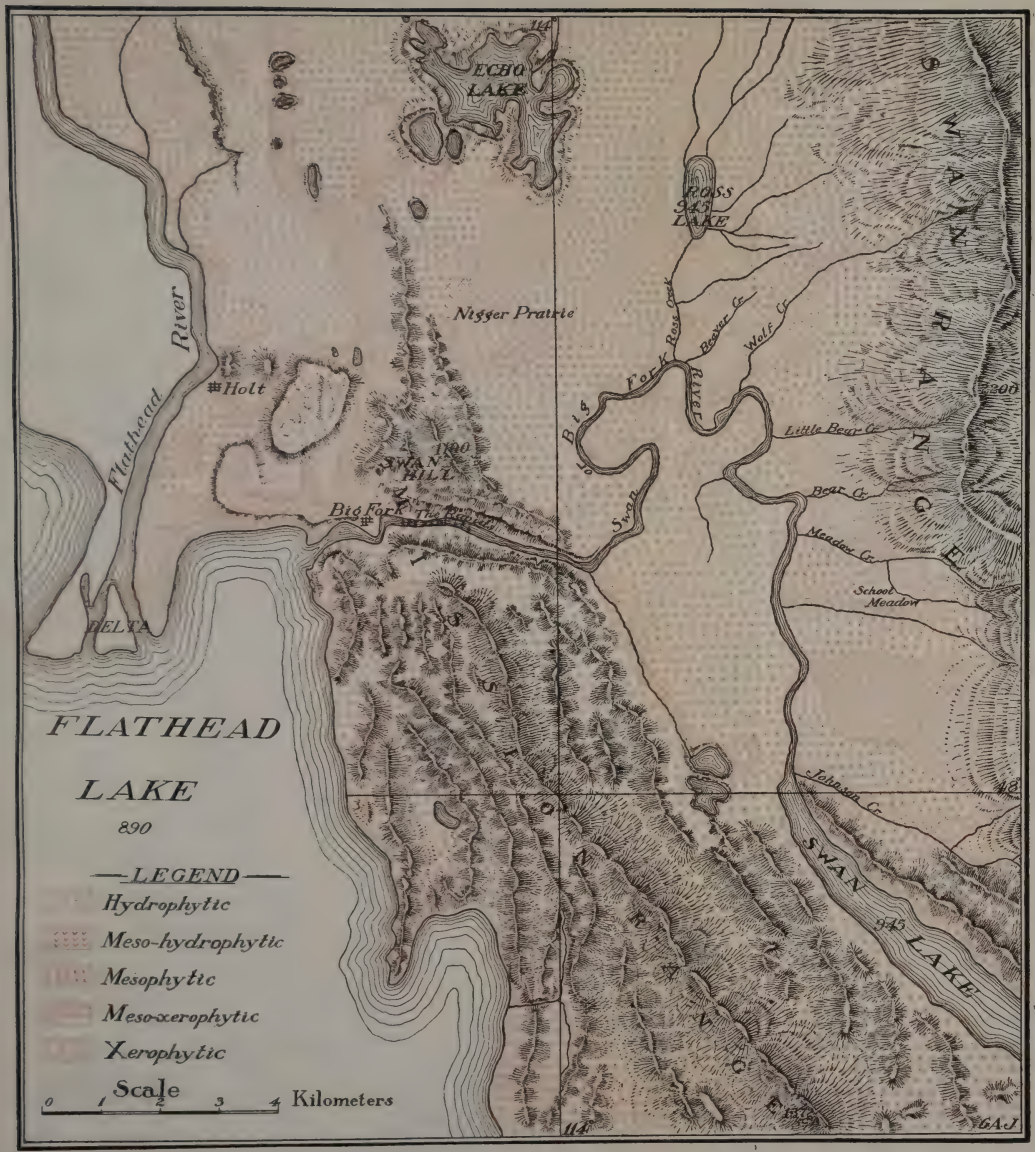


FIG. 2.—Map of northwestern portion of Montana, showing the general location of Flathead valley.—After ELROD.

valley varying in width from 16 to 40^{km}. The portion lying south of Flathead Lake is known as the Mission valley. That part with which this paper deals more especially is found in the region bordering the northeastern shores of Flathead Lake (*fig. 3* and *map*).

The main drainage system of the valley consists of the Flathead


ECHO LAKE
Nigger Prairie
Holt
Flathead River
SWAN HILL
Big Fork
DELTA
FLATHEAD LAKE
890
LEGEND
Hydrophytic
Meso-hydrophytic
Mesophytic
Meso-xerophytic
Xerophytic
Scale
0 1 2 3 4 Kilometers
Foss 945 LAKE
Big Fork River
South Fork Rose Creek
Beaver Cr.
Wolf Cr.
Little Bear Cr.
Bear Cr.
Meadow Cr.
School Meadow
Johnson Cr.
SWAN 945 LAKE
MISSION RANGE
SWAN RANGE
6A-J

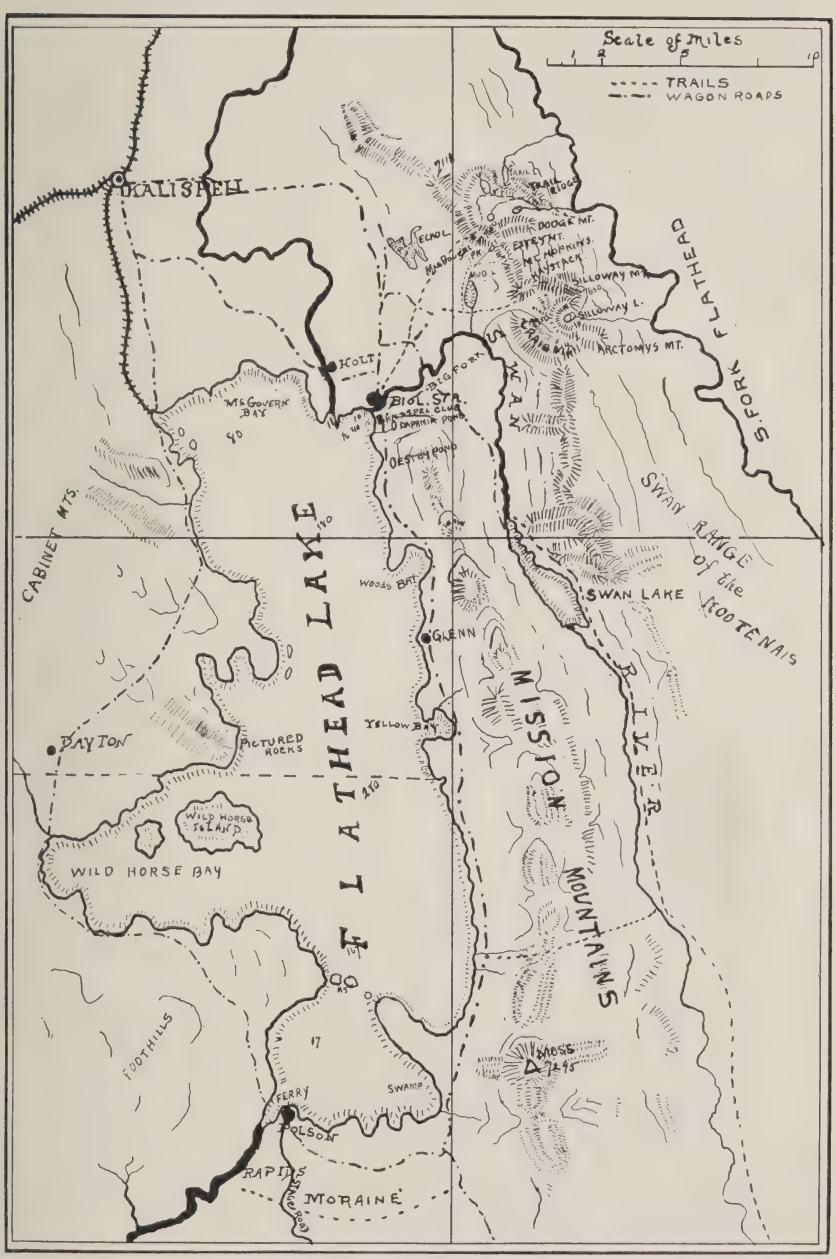


FIG. 3.—Map of Flathead Lake and adjacent region; compare with *fig. 1* and *map*.—After ELROD.

Lake; its principal inlet, Flathead River; and its outlet, the Pend d'Oreille River. Flathead River is formed by the confluence of three branches known as the North Fork, South Fork, and Middle Fork, all of which rise in the Rocky Mountains. These flow for their entire course in valleys in the mountains and unite to form the main river near Columbia Falls. The Stillwater and Whitefish Rivers are the principal branches that lie in the Flathead valley. For about the lower half of its course through the valley, the Flathead River is a broad, sluggish, navigable stream that is constantly depositing sediment. Especially is this the case at its mouth, where a delta about 3^{km} in length has been formed (*fig. 4*).

Flathead Lake (*fig. 5*) is some 40^{km} from north to south and varies in width from 10 to 20^{km}, its altitude being 890^{m}. It is a remnant of a former lake of much greater extent, which probably covered a large portion of the valley at its head. An old outlet near Dayton (*fig. 3*), some 120^{m} above the present level of the lake, and terraces at approximately the same height, indicate the former distribution of the waters of the lake. The Pend d'Oreille River (*figs. 5, 6*), the present outlet, has cut its way through a huge moraine at the foot of the lake. This moraine no doubt acted as the dam that backed up the water over the low valley lying to the north. The river rapidly cut its way through this moraine until its present condition was developed. This erosive process is going on much more slowly today because the river channel has reached bed rock.

The Mission Range lies to the east of the lake and the Mission valley. This is a distinct range separated from the other mountains on the east by the Swan River valley. It has an altitude of approximately 2750^{m} at its southern end. From this altitude the mountains become gradually lower until near the north end of the lake, where they merge imperceptibly into the valley. The Swan River valley opens into the Flathead valley where these mountains end (*map* and *fig. 1*). It is in reality only an arm of the latter, and during the time of the greatest extension of Flathead Lake the water probably backed up into this valley and formed an embayment. As the Pend d'Oreille River cut its way through the moraine at the foot of Flathead Lake, the level of the water in this embayment was lowered. But some time before the present condition was reached, a moraine

FIG. 4.—Looking west from Mission Mountains across the northern end of Flathead Lake; the delta is seen in the distance; on the right is the town of Big Fork near the mouth of Swan River; beyond Big Fork is a portion of the prairie region; in the center and on the left is the forested region on the west slopes of the Mission Mountains; the forests here have been nearly destroyed by fire.—From photograph by ELROD.

FIG. 5.—Flathead Lake looking north from moraine at south end; in the distance a chain of islands stretching nearly across and dividing the lake into two unequal parts, the greater portion being to the north; the islands mark the beginning of the forested region; to the left the outlet of Pend d'Oreille River, a part of which is seen in *fig. 6*.—From photograph by ELROD.

FIG. 6.—Pend d'Oreille River, the present outlet of Flathead Lake; the river has cut through moraine shown in *fig. 5;* as its channel was eroded the level of the lake was lowered, and the receding waters left broad areas of level land.—From photograph by ELROD.

FIG. 7.—Looking north from the south end of Ross Lake; in the deeper waters are *Nuphar advena*, *Brasenia purpurea*, *Potomageton* sp., etc.; around the borders are sedges and grasses; outside these is the Engelmann spruce formation; the meadow is submerged during the spring and early summer months.

was probably thrown across the mouth of the Swan valley, and thus its connection with the main lake was cut off. A gap in the Mission Range offered a favorable place for the water thus cut off to make its escape. This outlet, of course, marked the beginning of that portion of the Big Fork River known as the "rapids" (*map*). Just as the present condition of the drainage system of Flathead valley is only a stage in the history of the destruction of the former enlarged Flathead Lake, so the existing drainage system of the Swan valley is only a stage in the history of the destruction of the former more extended Swan Lake. This system consists of Swan Lake; its inlet, Swan River; and its outlet, Big Fork River. Swan Lake is a body of water some twelve miles long and, except at its upper end, very narrow. It passes almost imperceptibly into the Big Fork River. This is a meandering stream which with its branches drains the valley and the mountains lying to the east and west of it. With the exception of small rapids here and there, and that part of it known as the "rapids," the river is a rather sluggish stream. The valley (*fig. 8*) is approximately 945^{m} above the level of the sea. The Swan Range of the Kootenai Mountains rises abruptly from the east side of the valley to an altitude of from 1800 to 2200^{m}, and the Mission Mountains border the valley on the west.

Such, in brief, are the main features of the physiography of the Flathead valley and its arm, the Swan valley. More detailed peculiarities will be noted in connection with the discussion of the edaphic formations; for, as will be shown later, there is an intimate relation existing between the destruction of the two lakes and the development of the plant formations that are found in the valleys.

GEOLOGY.

Flathead valley is not, as one would suppose, an erosion valley, but according to WILLIS[7] it is due to a fault resulting in the downthrow of the region of the valley and an uplift of the region of the present Rocky Mountains. The northern Rocky Mountains consist of limestones, quartzites, and siliceous argillites about 2750^{m} thick. During pre-Cambrian times the whole was under water. At the beginning of the Cambrian age an uplift brought it above

[7] WILLIS, BAILEY, Structure of the front range, northern Rocky Mountains, Montana. Science N. S. **15**:86–87. 1902.

FIG. 8.—General view looking across the Swan valley from Mission Range; Swan Range in the distance; the forest in the valley is western larch-Douglas spruce type except where the lodgepole pine has come in after fires; in the foreground a portion of the Mission Range; the forests completely destroyed by fires.—From photograph by ELROD.

water, and during all the Palaeozoic and part of the Mesozoic the pre-Cambrian rocks were subjected to subaerial erosion. A movement at the close of the Jurassic again brought the sea over it. Then Cretaceous sediments of considerable thickness were deposited upon pre-Cambrian limestone and quartzite. In post-Cretaceous times a fold was overturned to the northeast. Some time in the Tertiary, probably during the Miocene, the faulting mentioned above occurred. The rocks tilt as a rule to the southeast, the northwest fault face of the rocks being very steep.

SUMMARY.

1. The Flathead valley is due to a fault, and is technically known as a rift valley.

2. The greater part of it was formerly occupied by a lake.

3. The present drainage system of the valley consists of the Flathead Lake, the Flathead River and its branches, and the Pend d'Oreille River.

4. The Swan River valley, an arm of the Flathead valley, has for its drainage lines the Swan Lake, the Swan River, and the Big Fork River with its branches.

5. These drainage systems are remnants of the former more extensive lake that occupied the valleys.

I. Climate of Flathead valley in relation to climatic formations.

It has already been shown that the climate determines the general plant formation of a region. It is important, then, that the elements of the climate be analyzed thoroughly, and it should be pointed out at the same time in just what way these elements affect the distribution of plants. In order to obtain a better understanding of the true relation of the forests of this valley, its climate will be compared with that of the northern peninsula of Michigan, where both deciduous and coniferous forests are found; and with that of the Puget Sound region, where the coniferous type of forest reaches its highest development.

There are meteorological reports from two stations in the Flathead valley. These reports, though meager in some particulars, will give a fair idea of the climatic conditions found in a prairie

formation and in a forest formation. The data collected from Kalispell, Montana, cover a period of from four to five years. This station is located in the prairie region of the valley. From a station at Columbia Falls partial meteorological data were obtained that will give an idea of the climate of the forested portion of the valley. Marquette, Michigan, was chosen as the station to represent the climatic conditions of northern Michigan; and Seattle, Washington, will stand fairly well for the kind of climate found in the Puget Sound region.[8]

TEMPERATURE.

The following table contains the latitude, longitude, altitude of the stations, the number of years data have been collected, and the mean annual and monthly temperatures (degrees Centigrade) for the four stations.

TABLE I.

Stations	Lat. Long.	Alt.	Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell.....	48° 10′ N. 114° 25′ W.	904^{m}	5	−4.0	−4.5	1.5	6.0	10.5	14.0	16.5	16.0	11.0	7.0	0.5	−2.0	6.0
Columbia Falls...	About same	946	5	−5.0	−4.5	0.0	6.0	11.5	14.0	18.0	14.0	10.0	6.0	0.0	−4.5	5.5
Marquette.....	46° 34′ N. 87° 24′ W.	224	29	−9.0	−8.5	−5.0	3.0	9.0	15.0	18.0	17.5	13.5	7.0	−0.5	−5.0	5.0
Seattle.....	47° 38 N. 122° 20′ W.	1.5	12	5.5	5.5	7.0	10.0	12.5	15.5	17.5	17.5	15.0	10.5	7.0	6.0	11.0

The significance of these figures will be clearer when it is known just how the temperature influences the various physiological processes. An examination of Table I and *fig. 9* will show that the mean monthly temperatures during the growing season is rather low as compared with regions farther south; also, during the months of May, June, July, August, September, the means for the four stations are not far apart; so that any difference in the type of vegetation in the four stations cannot be accounted for by differences in temperature during the so-called growing season. If the temper-

[8] The data given in the tables below were obtained from the following gentlemen in charge of the stations at their respective cities: Kalispell, Mont., H. B. DICK; Marquette, Mich., H. R. PATRICK; Seattle, Wash., G. N. SALISBURY. The figures for Columbia Falls, Mont., were obtained from the Climate and Crop Service Bulletin of Montana for 1900 and 1901. No sunshine records are kept at Marquette, so those from Escanaba, Mich., are taken to represent northern Michigan in that particular.

ature has anything to do with the difference in the character of the vegetation, it must be the temperature of the non-growing rather than of the growing season.

It is too often assumed that during the non-growing season physiological processes of plants are inactive.[9] Of course, this is true of growth; indeed, growth is checked and ceases rather early in the season; but photosynthesis is known to occur during the winter months. Experiments by MIYAKE[10] show that this process is active at temperatures in the neighborhood of 0° C. Among the evergreen leaves experimented upon were species of pine and spruce. One of MIYAKE'S conclusions is that starch is formed in winter, though

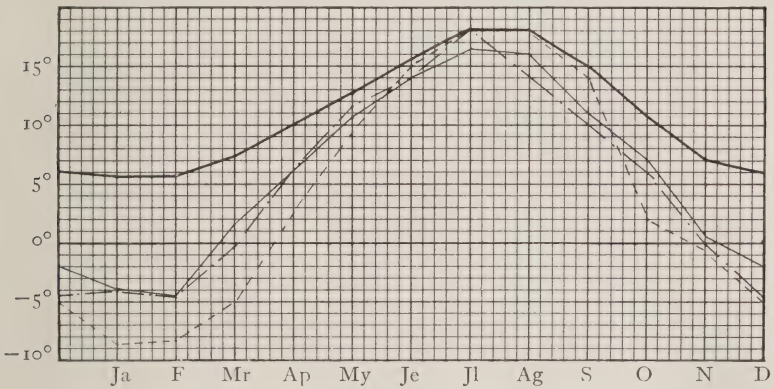


FIG. 9.—Comparative temperature for Seattle (———), Kalispell (— — —), Columbia Falls (——·——·), and Marquette (– – – – –); the figures are temperature Centigrade; winter temperature for Seattle comparatively high, for Marquette low, for Kalispell and Columbia Falls intermediate; summer temperature for all stations nearly the same.

in small amounts, and its translocation occurs in the same season. His work was conducted at Tokyo, Japan, where the mean temperature of the three winter months is as follows: December, 5.1° C.; January, 2.7° C.; and February, 3.5° C. If trees can do photosyn-

9 MERRIAM says that "in computing the sum of the positive or effective temperatures a minimum of 6° C. has been assumed as marking the inception of the period of physiological activity in plants and of reproductive activity in animals." MERRIAM, C. H., Life zones and crop zones of the United States. U. S. Dept. Agric., Div. Biol. Survey, Bull. 10: 4, note 2. 1898.

10 MIYAKE, K., On the starch of evergreen leaves and its relation to photosynthesis during the winter. BOT. GAZETTE **33**:321–340. 1902.

thetic work in the climate of Tokyo during the winter months, it is possible that more food is manufactured by the trees in the Puget Sound region, where the temperature is even higher than at Tokyo. If this be the case for the winter months, it will be even more so for the early spring and late fall months, when the mean temperatures at Seattle are as follows: March, 7.22° C.; April, 10° C.; October, 10.5° C.; and November, 7° C.

The evergreen trees, however, in a climate like that at Marquette would not be able to do so much work during these months, for the temperature is very much lower. In other words, in a climate with warm winters like that at Seattle, the evergreen trees can work more or less during the winter, early spring, and late fall months; while in a climate like that at Marquette, where the mean temperature is considerably below the freezing point during the winter months, this work would be very much checked if not stopped altogether. As one would expect, from this standpoint, the conifers would be more successful in the Puget Sound region than in the northern peninsula of Michigan. The conclusion that is reached from the foregoing is that, other things being equal, an equable distribution of heat is favorable to conifers. A reference to the temperature conditions in the Flathead valley will show that the climate is more equable than that at Marquette, but not so equable as that at Seattle. The coniferous forests are better developed here than at Marquette, but are not nearly so luxuriant as at Seattle. From the standpoint of carbohydrate manufacture, the deciduous trees are little or not at all affected by the temperature conditions of the non-growing season, for their leaves are absent, and consequently photosynthetic work is very much reduced.

A comparison of the temperature conditions at Kalispell and Columbia Falls shows a little difference, the latter being slightly colder. While this difference may affect herbaceous vegetation, it would likely have little or no effect on the forests; so the fact that there is no forest at Kalispell, while there is one near Columbia Falls will have to be explained on other than temperature grounds.

Transpiration, which also takes place during the non-growing season, will be discussed in another connection.

RAINFALL.

The greatest danger to trees is an excessive loss of water, and therefore the rainfall of a region is very important. It will be pointed out later how the conservation of this water supply influences the character of the forest. Other things being equal, the greater the amount of rain that reaches the earth, the more luxuriant the vegetation. The mean monthly and annual rainfall for Kalispell, Columbia Falls, Seattle, and Marquette are as follows, the amounts being given in millimeters:

TABLE II.

Stations	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell.....	24	25	16	21	69	47	33	28	50	18	49	35	415
Columbia Falls.....	48	38	36	33	66	72	37	31	68	30	54	30	543
Marquette.....	52	45	47	51	76	89	77	73	99	83	69	62	823
Seattle.....	111	94	79	82	86	40	17	14	45	76	143	158	945

The difference in the amount of rain on the west and east sides of Flathead valley no doubt explains the difference in the types of vegetation in these two situations. It has already been shown that there is only a slight difference in the amount of heat at the two situations. It is very probable that the other elements of climate—light and velocity of wind—are about the same for the two places, although there are no data to prove this. It must be remembered that the towns are only thirteen miles apart, but the difference in rainfall is 128^{mm}. It is believed that this difference is sufficient to make a forest vegetation at Columbia Falls and only a prairie vegetation at Kalispell. Kalispell is well out in the valley, while Columbia Falls is at the base of the mountains. The rain-bearing winds from the west sweep across the high mountains west of the valley, where they lose a considerable portion of their moisture, and then descend into the valley where the higher temperature they encounter enables them to hold more moisture. This is liberated, however, when the winds bank up against the cool mountains east of the valley. Thus the west side of the valley probably has a rainfall of 400^{mm} or less and is not able to support tree growth except along streams; while the east side has a rainfall of from 400 to 543^{mm}, a sufficient quantity

to enable forests to exist. It is very probable that farther to the east in the mountains there is a still greater quantity of rain. At least the character of the vegetation would suggest that this is the case, for here the forest growth approaches in luxuriance that of the Puget Sound region where the rainfall is much greater.

A comparison of the rainfall in the valley with that of the Puget Sound region and of the northern peninsula of Michigan will lead to some interesting conclusions (Table II and *fig. 10*). In this comparison the data at Columbia Falls will be used rather than those at Kalispell, for reasons that are at once apparent. The character of

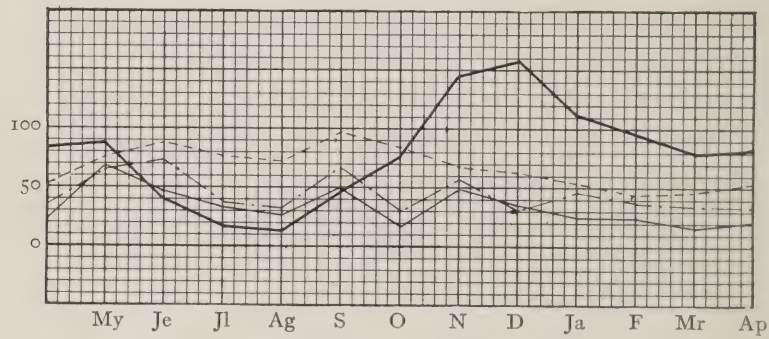


FIG. 10.—Comparative rainfall for Seattle (·———), Kalispell (———), Columbia Falls (——·——·), and Marquette (– – – – –); the figures are millimeters of rainfall; summer rainfall highest at Marquette and exceedingly low at Seattle; in winter rainfall the reverse is true.

the distribution of the rainfall is of considerable importance. Thus at Marquette and Columbia Falls the rainfall is more or less evenly distributed thoughout the year, with the five warmest months, May, June, July, August, and September, having about half of the moisture. Thus these five months at Columbia Falls show a fall of 274^{mm} out of a total of 543^{mm}; and at Marquette 414^{mm} out of 823^{mm}. On the other hand, Seattle with its total of 945^{mm} has only 202^{mm} during these months. It is a well-known fact that the broad-leaved deciduous trees evaporate more moisture during the summer months than do the narrow needle-like leaves of the conifers. It is very possible that the 202^{mm} at Seattle and even the 274^{mm} in the Flathead valley are not sufficient to maintain the broad-leaved deciduous trees in these climates. In any event, they are absent in the two

regions, except along water courses, and are present in the Marquette region where they are more successful than conifers.

The winter distribution of rain is of extreme importance, especially to those trees that hold their leaves, for KUSANO[11] has shown that evergreen leaves transpire considerably even at temperatures below freezing. While there are no data to show whether the bare twigs of deciduous trees transpire more or less than those of conifers, yet *a priori* it is very likely that they give off less moisture, for they have less surface. If this be the case, conifers are more in danger of desiccation during the winter months than deciduous trees; for even though the amount of evaporated moisture is slight, it must be remembered that the ground may be cold or even frozen, and that absorption is thus checked. However, if the rainfall is sufficient and the relative humidity of the atmosphere is high, this danger is less. The figures will show that the winter rainfall of the Puget Sound region is excessive, while that of the Flathead valley and the northern peninsula of Michigan is equal in quantity to the summer rainfall. Conifers exist in all three situations. The extensive rainfall in the winter months at Seattle must be coupled with the fact that the temperature conditions during these and the early spring months are exceedingly favorable to certain physiological processes and account for the almost tropical luxuriance of the trees of that region.

RELATIVE HUMIDITY.

The relative humidity of the atmosphere is another factor closely associated with the amount of rainfall. The drier the atmosphere the greater the transpiration. Other things being equal, the nearer relative humidity is to absolute humidity, the less water will the trees give off, and the less danger will there be of their desiccation. The greater the saturation deficit, the greater the danger of losing water. The following table will show the mean monthly deficits of the three stations to be considered. Unfortunately there are no data from Columbia Falls.

The high averages of the saturation deficit for July and August for Kalispell, together with the small rainfall, probably account for the

[11] KUSANO, S., Transpiration of evergreen trees in winter. Jour. Coll. Sci. Tokyo 00:313–366. 1902.

TABLE III.

Stations	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Kalispell	16.4	21.2	21.5	30.3	23.1	26.1	44.0	41.2	22.1	25.0	17.6	14.6
Marquette	16.5	16.4	19.7	23.7	27.0	27.0	27.6	23.3	22.3	19.8	17.5	17.4
Seattle	16.0	20.7	25.0	29.2	28.9	30.9	32.6	29.6	24.5	18.4	15.6	15.5

prairie condition there and on the west side of the Flathead valley. It must be emphasized, however, that the saturation deficit is of great importance only in connection with the amount of water available in the soil. If the ratio of the water obtained by the tree from the soil to that given off is $1:-1$, then the tree is in no danger of desiccation; if, however, the ratio is $-1:1$ or $1:1$, the tree is in danger of desiccation. From this it will be seen that if there is in the soil plenty of water that the tree can obtain, there will be tree growth though less luxuriant, even though the saturation deficit is high. This accounts for the existence of trees along streams even in prairie regions.

A comparison of the atmospheric deficits of Marquette and Seattle reinforces what was said concerning the rainfall of these two regions. It will be seen that both have a fairly low atmospheric deficit during the winter months, thus decreasing the possibility of transpiration at a time when the ground is cold. In the Puget Sound region the comparatively high temperature renders greater transpiration more likely than in the Marquette region, but this is offset by the fact that the temperature of the soil is no doubt warm, thus rendering available for absorption some of the great amount of water that reaches the soil in the form of rain during these months.

Again, a comparison of the atmospheric deficit data for the five growing months of the year shows a uniformly higher deficit for Seattle than for Marquette. This coupled with the fact that Marquette has a rainfall of 414^{mm} during these months against 202^{mm} for Seattle makes deciduous forests possible in the former region, but not in the latter.

VELOCITY OF WIND.

Another climatic factor that is likely to play a part in the distribution of the forest is the velocity of the wind. Perhaps the great-

est influence the wind has on trees is to increase the transpiration, and they more than any other form of vegetation are subject to the drying effects of winds. Indeed so important does SCHIMPER (pp. 542–555) think this factor that he considers it influential in bringing about the prairie condition. Below is given the mean monthly and annual wind velocities for the three stations. Again, there are no data for Columbia Falls, but the amount of wind is probably not very different from that at Kalispell. The figures are in kilometers per hour.

TABLE IV.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann'l
Kalispell.....	7.4	7.7	9.5	10.4	10.0	10.1	10.0	9.6	9.0	8.2	7.2	7.2	8.8
Marquette.....	17.3	16.1	16.7	15.4	16.2	12.6	13.8	14.2	16.2	18.0	17.7	18.0	15.9
Seattle.....	10.3	11.1	10.9	10.4	9.5	9.0	7.6	6.6	7.4	8.0	10.1	10.7	9.3

As shown from these figures, one of the remarkable facts about the Flathead valley is the absence of excessive wind. It is believed that this, coupled with the rather low mean monthly temperature for the summer months, is what makes possible so luxuriant a forest, with a rainfall of about 500^{mm}. In passing from the east side of the Rocky Mountains into the Flathead valley, the decrease in the amount of wind is very noticeable. Thus, Kipp on the east side of the Rocky Mountains has a normal rainfall of 512^{mm}, yet it has no tree growth. Although there are no data to show that there is more wind here than in Flathead valley, the fact is very apparent to one who has been in the two regions. It is believed that the excessive winds prevent the growth of trees, in spite of the fact that there is a rainfall of about 517^{mm}, or nearly as much as at Columbia Falls.

Compared with Marquette the wind velocity of Seattle is low. This would again favor a more luxuriant vegetation in the latter region than in the former.

SUNSHINE.

The more light, other things being equal, the more work trees can do. On clear days more food is manufactured than on cloudy days. This process can go on, as has been shown, during the non-growing season when the temperature is not too low, though the

amount of food manufactured then is much less than at higher temperatures. Light is the least variable of all the climatic elements. Possibly for a given altitude and a given latitude the variability is not great enough to have much influence on the kind of vegetation. However, the sunshine data may prove of importance in comparison with other regions. In the table below the mean possible hours of sunshine, which would be the same for a given latitude, and the mean actual hours are given. The observations cover a period of short duration.

TABLE V.

	JANUARY		FEBRUARY		MARCH		APRIL	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell	276.2	88.2	286.8	111.8	370.1	180.7	410.4	240.2
Escanaba	283.1	85.3	290.4	120.5	370.3	129.8	407.0	178.4
Seattle	276.2	66	286.8	103.8	370.1	168.6	410.4	205.2

	MAY		JUNE		JULY		AUGUST	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell	471.3	231.4	479.8	279.6	483.2	364.4	442.5	269.6
Escanaba	464.1	163.8	471.7	218.7	475.7	211.5	437.6	230.5
Seattle	471.3	226.9	479.8	248.5	483.2	301.7	442.5	257.5

	SEPTEMBER		OCTOBER		NOVEMBER		DECEMBER		ANNUAL	
	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.	Poss.	Act.
Kalispell	377.5	202.5	335.8	174.6	278.0	73	262.1	49	4473.7	2262.9
Escanaba	376.1	149.1	338.5	148.8	284.1	52.9	269.6	61.4	....	1727.1
Seattle	377.5	186	335.8	110	278	40.6	262.1	45	4473.7	1959.6

In his classification of climatic formations, SCHIMPER (pp. 556–565) does not recognize a distinct formation for the coniferous forest, placing it in what he calls the summer-green forest (deciduous). There is little doubt that he is right so far as the eastern part of the United States south of the latitude of Lake Superior is concerned. Here, as shown by COWLES (*l. c.*) and the writer (*l. c.*), the conifer-

ous forests occur as edaphic formations in the summer-green climatic formation. In this region they are xerophytic formations (societies) forming a stage in the progression toward the climax mesophytic deciduous forest formation. With the wearing down of the xerophytic hills, the filling up of swamps, and the accumulation of humus on the sandy plains and hills, the coniferous societies which now prevail there will give way to the climax deciduous forest, which is the highest expression of a climate similar to that found in the eastern United States.[12]

The Pacific coast district north of San Francisco, and including the moister mountainous regions inland, presents a climate entirely different from that of the eastern United States. Here, as compared with the eastern deciduous forest region, there is a more equable distribution of temperature throughout the year, with winter rains and excessively dry summers. The forests here are coniferous, with the deciduous element occupying only edaphic situations along water courses. It is my belief that in some such climate as that found in the Puget Sound region the coniferous forest is at its best, the deciduous type being unable to compete with it because of the dry summers.

The climate and character of the vegetation of the Pacific coast region corresponds more nearly with SCHIMPER'S sclerophyllous woodland (pp. 464–469, 507–540) than they do with his summer-green climate and vegetation. Indeed, elements of the sclerophyllous vegetation are found in the Puget Sound district, for here such trees as *Arbutus Menziesii* show a type of leaf decidedly like that found in climatic districts which SCHIMPER has so aptly called sclerophyllous woodlands. The sclerophyllous formations are in a climate with winter rain and comparatively high and equable temperature. Likewise the Pacific coniferous district has winter rains and a comparatively equable temperature, that is rather warm winters and cool summers. However, the mean average monthly temperature is much lower than that of the sclerophyllous districts of the warm temperature belt. This is no doubt influential in bringing about the narrow type of evergreen leaf rather than the broad type found in the warmer climate.

[12] See SCHIMPER (p. 545) for table showing rainfall of Atlantic forest district and Pacific coast.

For reasons given above, it is my belief that SCHIMPER'S summer-green climatic formation should not include the coniferous forests of the Pacific coast of North America, but that these should be separated from it. In order to show its relations to the broad-leaved sclerophyllous formation, I would suggest that it be called the *needle-leaved sclerophyllous formation.* The limits of this formation are not clear. While no doubt it reaches its best development in the Puget Sound region, this does not prevent its spreading into more northerly regions with cooler but still damp winters. Whether this type is the climax forest formation in the region north of the Lake Superior district, as it is on the Pacific coast, or only edaphic formations in the summer-green climatic formation of the United States, our present knowledge cannot determine.

The forests of the Flathead valley clearly belong to the needle-leaved sclerophyllous formation, but since they are on the border of a prairie climate they are not so good an expression of it as is that of the district farther west

THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

[*Continued from p. 122.*]

II. EDAPHIC FORMATIONS IN FLATHEAD VALLEY.

IN the previous pages an attempt was made to show why the west side of the valley contains a prairie formation, and the east side a forest formation, and why the coniferous type of forest prevails rather than a broad-leaved deciduous type. A plot will now be presented in detail to show why in the forest formation there are some areas altogether without trees. In order to reach definite conclusions, a limited area was selected to represent the whole forest area of the valley. This area, comprising about 250 square kilometers, was mapped, and the conditions for forest growth were determined (*map*). The relation of this area to the whole valley is shown in *fig. 3*. It lies at the northeast end of Flathead Lake, and includes a portion of the main valley on the east side of the Flathead River at the head of the lake, the low end of the Mission Range of mountains, and a portion of Swan valley. In this area are found many types of topographic diversity, from Flathead Lake (890 m) to the highest point (about 1372 m) in that part of the Mission Range which is included in the map. No detailed study was made in the higher Swan Range east of the valley, though some conditions of tree growth were noted in these mountains. As shown by the map, five distinct edaphic formations were found: meadow (*hydrophytic*), Engelmann spruce (*meso-hydrophytic*), western larch-Douglas spruce (*mesophytic*), Douglas spruce-bull pine (*meso-xerophytic*), and prairie (*xerophytic*).

THE MEADOW FORMATIONS (HYDROPHYTIC).

As already mentioned, Swan valley was formerly a lake, the present condition being only a stage in its recession. The drainage consists of Swan Lake, Big Fork River, and a number of small

streams; also one large pond known as Ross (Mud) Lake, which, with its outlet Ross Creek and the numerous small inlets, comprise the drainage of the extreme north end of the valley.

The most noteworthy fact about the hydrophytic vegetation is its resemblance to that found in similar edaphic situations in the eastern United States, both types of swamps being found here. Near the head of Ross Lake is a sphagnum meadow, in which *Menyanthes trifoliata*, *Drosera rotundifolia*, *Comarum palustre*, *Eriophorum polystachyon*, and *Betula pumila* are characteristic. At least two other large meadows show this combination. One of these is along Little Bear Creek, and is known as the School Meadow; another is found along Flathead River, and will be discussed in connection with the spruce forest which lies close to it. Ross Lake (*fig. 9*) is a pond which shows very well the zonal distribution of plants, being shallow and with a very muddy bottom. In its center and in streams bordering it are found the following characteristic species: *Nymphaea advena*, *Brasenia purpurea*, four species of Potamogeton, Myriophyllum, and Hippuris. The sedge zone bordering the water of the shallow ponds and streams contains the following species: *Bromus Richardsonii pallida*, *Muhlenbergia racemosa*, *Carex utriculata*, *C. viridula*, *C. hystricina*, *Calamagrostis caespitosa*, *Phalaris arundinacea*, *Juncus Regelii*, *Scirpus lacustris occidentalis*, *Lobelia* sp., *Cicuta maculata*, *Solidago* sp., and *Dodecatheon* sp.

The meadows are usually submerged during the spring and early summer months, when the melting snow of the mountains to the east swells the streams, and brings the water level slightly above the surface. In the latter part of the summer and fall the underground water level is a little below the surface; and it is this condition of submergence and emergence that determines the meadows and excludes trees. Of course some of these meadows are never entirely submerged, but are always wet, with few exceptions being associated with streams. The largest meadows are found near the head of Ross Lake, at its foot on the east side, near the mouth of Wolf Creek, at the foot of Swan Range along Little Bear Creek, and in the large bend of the river just east of Swan River cañon.

The meadows are given brief mention here in connection with this forest study because they are genetically related to the spruce

forests that usually border them. It is obvious that trees do not grow in them because the amount of moisture in the soil is too great. Some of the meadows have been artificially drained, others have been planted to timothy, and one in particular, in the northwestern corner of the area (*map*), has been drained and cultivated for a number of years, so that its former nature was discovered with difficulty. What has been done artificially is being done naturally, but more slowly. The detritus that is washed into the ponds and the vegetation that dies down from year to year are filling up these bodies of water, and are making the meadow condition possible. Again, the streams are cutting their channels deeper, thus lowering the underground water level at their borders, and this changes conditions that favor meadows and introduces those that make the forest possible. It is very probable that many areas now occupied by spruce and other forests were formerly occupied by meadows. Indeed, all stages of development towards this forest condition were noted, and will be discussed under the next head.

THE SPRUCE FORMATIONS (MESO-HYDROPHYTIC).

In many places species of Salix and *Alnus incana* encroach upon the meadows, sometimes forming dense breastworks around the grass areas, so that it is difficult for other trees to get a start. This is the case when the zones of underground water level are sharply and narrowly marked off. Usually, however, when the underground water level is at a fairly uniform distance below the surface for a rather broad area, as it is where the small streams spread out over a level extent of land, the willow-alder breastwork is absent. These situations are favorable for the advance of *Picea Engelmanni* into the meadows. The youngest trees are found on the hummocks in the meadows; nearer its borders are the older ones, though they are still scattered; these grade imperceptibly sometimes into dense forests of spruce, many of the trees reaching huge dimensions. Since this formation is found best developed on situations where the underground water level is a little farther below the surface than it is in the meadows, it may be called the meso-hydrophytic formation.

It must not be supposed that there are no other trees with the spruce; indeed there are only small tracts where pure spruce woods

are found. The most common companion trees are *Populus angustifolia*, *Populus tremuloides*, and *Betula papyrifera*. These species nearly always form a small per cent. of the spruce forests, and in the meso-hydrophytic area along the Flathead River they occupy nearly the entire space. In Swan valley the soil is a mixture of clay and humus; along Flathead River, especially in the delta region, the subsoil is sand, overlaid by a fine alluvial deposit. In the dense woods the undergrowth is scanty, sometimes only one or two species being present, the most common plant associated with the pure spruce growths being *Rhamnus alnifolia*, although *Cornus stolonifera* is often found. In the narrow strip of this forest along the streams nearer the mountain *Echinopanax horridum* and *Veratrum californicum* are present. Since the spruce woods are transitional between the meadow and the mesophytic woods, the undergrowth of these associations is often present. Thus, near the meadow side of the forest, grass plots are frequently present, and on hummocks between anastomosing channels *Lysichiton kamtschatcensis* is frequent. On the other hand, toward the mesophytic side of the forest the elements of the undergrowth of the western larch-Douglas spruce formation are to be found.

An area of spruce is found in connection with a meadow in the northwestern corner of the plot not far from the Flathead River. Here on the border of the prairie formation is an area that has almost identically the same plants as the spruce forest in the Swan valley. Along the east side of this swamp there are numerous springs, some large enough to give rise to small streams, and others hardly noticeable. The source of the water supply is thought to be Echo Lake, which, with a number of smaller ones, lies in the depressions of a moraine that extends beyond the limits of the plot to the northeast. Save a small stream, there is no visible inlet to this lake, and its source of water supply is probably by underground seepage from the mountains that lie northeast. There is also no outlet above ground, and since the drainage is toward the Flathead River it is thought that the springs mentioned are fed by underground seepage from these lakes and ponds. This underground water level, as shown by the wells in the neighborhood, is in places nearly a hundred feet below the surface, and extends underneath the larch-Douglas spruce

and bull pine forests and the prairie to a low ridge near the Flathead River, where it issues in the form of springs, making conditions favorable for an Engelmann spruce formation. Thus a bit of forest is projected, as it were, into the prairie formation. Where the water level comes nearer the surface the meadow already mentioned is associated with the forest.

Another meso-hydrophytic forest in which the spruce is almost entirely wanting needs to be mentioned. Around the head of Flathead Lake, including the delta at the mouth of the river (*figs. 1* and *4*), and extending up the river from its mouth, is a region that is annually submerged.[13] This region is occupied by a dense growth of willows, cottonwoods, birch, aspen, and other trees. On each side of the mouth of the river are long, low peninsulas of sand, the ends of which are entirely barren of vegetation. These are above water only a short time during the growing season, and this fact no doubt prevents plants from getting a start. A short distance back from the end of the delta on a little higher land is *Salix fluviatilis*, in some places so thick as to be almost impenetrable. Underground stems are sent out from this center, and thus new territory is gradually conquered, so that as fast as the delta is built out it is occupied by this pioneer willow, which prepares the way for changes that make it possible for higher forms to exist. When the water is high its contact with the willows causes a deposit of fine silt, so that the delta is gradually built higher and higher, making conditions favorable for the growth of such plants as the red dogwood, other species of willow, narrow-leaved cottonwood, paper birch, aspen, choke cherry, two species of hawthorn, and service berry.

Around the head of the lake there is a low terrace which is also submerged in the spring and early summer months. Instead of *Salix fluviatilis* there is a thicket of other willows; and on the lake side of this there are a few scattered specimens of *S. fluviatilis* and *S. amygdaloides*. On the land side of the willow thicket are the birch,

[13] During the spring and early summer months Flathead Lake and River rise some 4 to 6m, submerging all the surrounding low country. In some instances excessive floods do great damage to the country lying at the head of the lake. Since nearly all streams in the valley have their sources in the mountains to the east, the deforestation of this region would greatly increase these spring floods and greater damage would be the result.

cottonwood, and aspen; and here and there are found small patches or single specimens of the western larch, Engelmann spruce, Douglas spruce, and bull pine. None of these were noticed on the delta proper, and with the exception of the Engelmann spruce they seldom occupy the areas that are often submerged. Of course in the lowest places the meadow type of vegetation prevails, and elements of it are scattered more or less through the area occupied by the trees. As already shown, the lake formerly extended over the valley north of it, and as its waters receded it is very probable that vegetation similar to that found around its shores today occupied similar areas around the shore line of the former lake. Of course as the gradual lowering of the underground water level brings about unfavorable conditions for those plants that exist around the shores, these are replaced by those needing other conditions. On that portion of the shore line that borders the area where the rainfall is insufficient to support trees, the swampy areas will pass through the meadow, the cottonwood-birch-aspen type, to the prairie. However, if the shore line be in a region that has sufficient rainfall to support a forest, the first two stages will be followed by a western larch-Douglas spruce-bull pine stage.

Since the Engelmann spruce is the most prevalent and the most important tree in the formation just described, its sylvicultural habits will be summarized. It has been shown that it does best in soils where the underground water level is not far below the surface, that is, for the plot under consideration, in low-lying lands bordering lakes, ponds, or streams. Thus it occurs not only in Swan valley, but also along the banks of Flathead River, where it is somewhat sparingly mixed with cottonwood-birch-aspen groups. It is the first tree to advance into the meadows. However, the Engelmann spruce is not confined to the more or less swampy region, for it is found scattered through the mesophytic areas in Swan valley. In the stands that lie adjacent to the spruce forests it is almost always present, and in some places it extends well out into the drier parts of the western larch-Douglas spruce formation, being found beyond the limits of the silver pine and lowland fir, and having a wider life range than either of these two species. It was often observed in the bull pine-Douglas spruce association where depressions in the topog-

raphy brought the surface of the soil near the underground water level, and along streams. However, trees in these situations seldom reach large dimensions.

The Engelmann spruce can tolerate shade fairly well; in this respect it is different from western larch and Douglas spruce and is classed with silver pine and lowland fir. The fact that it can endure shade probably accounts for the presence of its seedlings in the forests that occupy the drier areas in the plot, for the forest canopy in these situations brings about a local climate that makes it possible for trees to exist that could not otherwise do so. The Engelmann spruce has the power of germinating in the open if there is sufficient soil moisture, and like the other shade-enduring species it does better in these situations than in the shade.

It will be seen from the foregoing that outside the semi-hydrophytic conditions Engelmann spruce does not flourish in the plot under discussion, being confined to the level stretches of land bordering on the meadows and open bodies of water. There is little doubt that as the waters of the former Swan Lake withdrew, meadows first occupied these areas and then were replaced by spruce stands. Just as the meadow conditions may be considered the first stage in the development toward the climax forest of the region, so the spruce forest may be considered the second stage. As the channel of Swan River is cut deeper the water level of the valley will be lowered, thus bringing about a condition favorable to the development of other types of forest which will replace the spruce association.

In the above account the distribution of the Engelmann spruce is discussed only in the area mapped. In the mountains bordering the area on the east it shows a wide altitudinal range, but is always associated with good moisture conditions, for it is found best developed in the damp cañons and on damp slopes where it is invariably associated with *Abies lasiocarpa*. In the high basins it does not do so well as the fir, but in the lower valleys it flourishes where the alpine fir does not.

THE WESTERN LARCH-DOUGLAS SPRUCE FORMATIONS (MESOPHYTIC).

In the discussion of the Engelmann spruce formation it was shown that on its borders and on the dry hummocks in stands of this tree other trees obtained a foothold. Just as there is a gradation from

the meadows into the meso-hydrophytic forest in which the Engelmann spruce predominates, so there is a similar change from these into a forest in which the western larch and Douglas spruce are the principal trees. Again, this difference is due to a change in the underground water level; in the meadows it is near the surface; in the Engelmann spruce stands it is slightly below the surface; and in the western larch-Douglas spruce combinations it is still farther below. Indeed, in this association the water level is so far below the surface in places that the roots of the trees do not reach it, but rather depend on the water in the surface layers that comes from the rains or by capillarity from the underground water level. Since there is a medium condition of water in the soil, the forests occupying these areas are known as the mesophytic formations (*fig. 8*). Other trees found with *Larix occidentalis* and *Pseudotsuga taxifolia* are *Pinus Murrayana*, *Abies grandis*, *Pinus monticola*, *Picea Engelmanni*, *Thuja plicata*, and occasionally *Abies lasiocarpa*, *Pinus ponderosa*, and *Tsuga heterophylla;* also certain deciduous trees.

Associated closely with the spruce and almost invariably surrounding stands of it, except where the lodgepole pine is present, is found a forest in which the silver pine and lowland fir are at their best. Thus on the west side of the bay-like area of meso-hydrophytic forest west of Ross Lake, the spruce is gradually replaced by a magnificent growth of lowland fir, silver pine, western larch, and Douglas spruce. The lodgepole pine occupies a good deal of the spruce stands that would otherwise have developed into a forest like that just mentioned, were it not for the influence of fires. In various other areas are found forests in which silver pine and lowland fir form a more or less conspicuous element, especially in the area near the mouth of Meadow Creek. They are never unaccompanied by other species and seldom become the dominant trees, probably because the climate is not so congenial to them here as to some of the other dominant species.

The silver pine closely resembles its relative the eastern white pine. As already stated, in Flathead valley it does its best in the conditions surrounding the spruce stands, or where the water level is not far below the surface. However, it spreads over nearly all the mesophytic region in Swan River valley and ascends the east slope

of the Mission Mountains in moist situations. In the swampy soils silver pine has a shallow root system and is easily blown over by winds, many large trees being observed lying prostrate with nearly the entire root system exposed. Where the soil has sufficient moisture, this tree can germinate in the open with no shade whatever, but it can pass the seedling stage in rather shaded conditions. The only two trees that have a shade too dense for it are the giant arborvitae and the western hemlock. While it can exist in the shade around the drier edges of the mesophytic forest, it fails utterly to maintain a stand in the mature growth of these areas, and except in extremely favored places the silver pine cannot be considered a successful tree for the region under consideration. It succumbs easily to fires, many instances being noted where fires had swept through the forests destroying the silver pine, while such trees as western larch and Douglas spruce were only slightly damaged.

The distribution of lowland fir is very much like that of silver pine, both reaching their climax growth in about the same situations. Where the water level is rather far from the surface it is more successful than silver pine in the low altitudes; but its altitudinal range is less than that of the latter. It is able to develop in open places, in soil so dry that silver pine is excluded. Where the moisture was sufficient it was not an uncommon thing to find stands of small (3 to 5^m high) trees so dense that absolutely all vegetation was lacking beneath them. It is more tolerant of the shade than is silver pine, and because it can grow in drier soils it extends as undergrowth into the borders of the meso-xerophytic regions, where silver pine is seldom if ever found. Like silver pine and Engelmann spruce, the range of this tree is extended because of the protection of the forest canopy, but this is not the region of its best development. The largest trees seen were less than a meter in diameter and not more than 38^m in height. SARGENT reports that it attains its best development along the Pacific coast in Washington, Oregon, and northern California, where it is frequently $75–90^m$ in height.

By far the most successful tree in Flathead valley is western larch. It is a tree that closely resembles its eastern relative (*Larix laricina*) in general appearance, although its habits are decidedly different (*fig. 11*). As already shown, it is one of the first trees to gain a foot-

FIG. 11.—View of interior of a western larch-Douglas spruce forest near Big Fork, Montana; the undergrowth consists of *Acer glabrum*, *Philadelphus Lewisii*, *Holodiscus ariaefolia*, etc.—From photograph by MCCALLUM.

hold in the spruce association, where it is found on the ridges and hillocks, and it forms an important element in the neighboring forests. There are extensive areas in Swan valley where this is decidedly the predominating species, and on the west slope of the Mission Range in some places there are almost pure stands. It extends out into the prairie regions along the river courses and on protected slopes. It does not grow in as dry soils as Douglas spruce and bull pine, and hence is more restricted in its distribution in regions where the rainfall is slight. The young trees, unlike those of silver pine and lowland fir, cannot endure shade. In no instance was a seedling observed growing in the shade of a forest. Other things being equal, it does best in broad open places, although it can do fairly well in slight openings where the sunlight enters at least during the middle of the day. The western larch then does not tolerate shade and cannot reproduce itself unless an opening be made first in the forest. This may be done in the mature primeval forest by the dropping out of old trees, but more frequently accidents such as fires and winds bring about open places suitable for its reproduction, provided of course seed-bearing trees are left to stock the soil with seeds. In contrast with silver pine and lowland fir, it may be called a fire-resisting tree. Its thick bark enables it to withstand fires that would kill silver pine and lowland fir, old trees often being found still living in the midst of burned areas. Sometimes isolated trees stand towering over the young lodgepole pine growth that has come in after fires (*fig.* 12), and the only young trees competing with lodgepole pines are western larch.

Observations on the rooting habits of trees are in any case difficult to obtain, unless windfalls are frequent. Many trees of western larch were found standing in windfalls where silver pine, lowland fir, and Engelmann spruce had been blown over. From this one would judge that its roots penetrate much deeper than the roots of these trees; indeed this may be one of the reasons why western larch is able to exist in drier areas than can some other trees, for a deep root system will enable it to reach nearer to the underground water level or at least below the superficial dry surface layers where a tree with shallow roots could not get sufficient moisture.

Since Douglas spruce is a successful tree in the regions bordering

on the prairie, a discussion of its sylvicultural habits will be deferred until the meso-xerophytic forest is described. It is almost invariably

FIG. 12.—Three generations of forests in a "burn" near Ross Lake; first generation represented by isolated old specimens of western larch; second generation consists of a forest of lodgepole pines mixed with a few individuals of western larch; in the foreground is the third generation, which consists almost entirely of young trees of lodgepole pines.—From photograph by PRAEGER.

a companion of western larch in the mesophytic area, hence the name western larch-Douglas spruce association.

The giant arborvitae is another tree that needs brief mention here. In the plot under discussion, along the base of the Swan Range there are three isolated places where the arborvitae was noted. It is usually found in moist places and probably ought to be considered as a meso-hydrophytic rather than a mesophytic tree (*fig. 13*). West of the Cascade Mountains, where it reaches its greatest development, it is distinctly a tree of the moister regions.

Another tree found in Swan valley is alpine fir, mentioned before as associated with Engelmann spruce in the moist cañons of the mountains. From here it spreads to the subalpine regions where it occupies a prominent place in the basins where snow lies all the year. In places it also finds its way into the lower altitudes in rather moist situations, as in Swan valley. The birch maintains a place throughout the mesophytic area; especially is it frequent in the moister situations and mixed with the lodgepole forests.

The soil in the mesophytic area is variable in nature, the character of the vegetation changing to a certain extent with the variations. It is probably not the chemical composition that determines the kind of forest, but rather the physical composition, the capacity of the soil for holding water being the controlling factor. If the underground water level is not far below the surface, it makes little difference whether the soil is sand, clay, or gravel, so long as there is sufficient humus to furnish the needed nitrates. However, back from the low-lying lands, where the water level is too far below the surface to be reached by the roots of the trees, the physical character of the soil plays an important rôle. As a rule the soil of the valley is made up of clay, probably derived from the decay of the dolomitic shale, the principal rock of the surrounding mountains. This has been washed in and deposited in the bed of the former more extended Swan Lake, and is mixed more or less with silt. Humus has accumulated in places, and this is more abundant where fires have not been so prevalent; for not only do fires destroy the humus, but in the open places left after the destruction of the forest it dries out rapidly. In contrast with the rich beech and maple woods of the eastern United States, the humus content of the soil is considerably less in these coniferous forests. This is of course due to the fact that the needle leaf of the conifers is not so good a humus producer as the

FIG. 13.—Giant arborvitae forest in an inlet of Sinyalcamin Lake, in a part of the Mission Mountains not in the plot mapped; the young trees under the old stand are all arborvitae, as no other species can exist in so dense a shade.—From photograph by HAMILTON.

broad leaves of the maple, beech, and other deciduous trees. In places, however, considerable quantities of humus are present, especially where the trunks of fallen trees have been allowed to decay and have not been destroyed by fire. A very good indication of a soil rich in humus is the number of species of fungi and mycotrophic seed plants found in it; *Monotropa uniflora*, *Pterospora Andromeda*, and *Corallorhiza multiflora* being scattered rather thickly throughout the forest. However, one misses the rich array of fleshy fungi found so abundantly in the leaf mold of the deciduous forests. Except in those places where arborvitae, hemlock, and lowland fir are prominent, the shade is not very dense; and under the rather thin canopy of the other conifers there is enough light to permit the development of a number of semi-shade species.

A woody plant that gives a decided tone to the undergrowth throughout the mesophytic area and to some extent in the meso-xerophytic area is the dwarf maple (*Acer glabrum*), the only representative of the maples found in Flathead valley. It can hardly be called a tree, for it seldom becomes more than 3^m in height. Other characteristic shrubby plants are *Salix* sp., *Philadelphus Lewisii*, *Holodiscus ariaefolia*, *Amelanchier alnifolia*, and *Symphoricarpos* sp. In some places, usually more mesophytic, *Menziesia urceolaris* and *Taxus brevifolia* are found. Some of the forms, like snowberry, service berry, and mock orange, become more frequent as the forest becomes more open. Among the prominent more lowly forms were noted the following: *Berberis aquifolium*, *Aralia nudicaulis*, *Cornus canadensis*, *Chimaphila umbellata*, *Pyrola rotundifolia*, *Linnaea borealis*, *Rubus parviflorus*, *Clintonia uniflora*, *Adenocaulon bicolor*, *Tiarella unifoliata*, *Lycopodium* sp., and *Disporum* sp.

At the south end of Swan Lake, on the west side of Big Fork River, is an area with a soil decidedly pebbly, and probably of glacial origin (*map*), its inability to hold water being indicated by the character of the forest it supports. The Douglas spruce is about the only mesophytic tree found here, and in places there are groves of bull pine. On the east side of the river, so persistent is the absence of other species than Douglas spruce and bull pine, that the area was mapped as meso-xerophytic forest rather than mesophytic. It is rather open, and the vegetation in it becomes somewhat prairie-like;

indeed everywhere that the mesophytic forest grades into the Douglas spruce-bull pine combination the forest floor has prairie plants rather than forest forms.

It has been shown that the western larch-Douglas spruce association is found in those areas where the amount of water in the soil is less than in the areas that support the spruce formation. Again, attention must be called to the fact that in the former extension of the lake many parts of the valley now having mesophytic forest were moist enough to support spruce forests, and as the water of the lake receded the amount of water in the soil became less and less until the encroaching mesophytic forests crowded out the spruce forests. As there is a relation in origin, therefore, between the meadows and the spruce forests, so there is also a genetic relation between the spruce forests and the western larch-Douglas spruce forests. In places where the hills end precipitously near the lake shore, as on the west side of Swan Lake for instance (*map*), this relation is not so apparent, for the mesophytic forests reach in many cases to the water's edge. Yet even here narrow, flat areas at the foot of the mountains on the borders of the lake have small meadows with scattered Engelmann spruce and cottonwood in them. These will give way, of course, to the encroaching mesophytic element when the waters of the lake have further withdrawn.

In conclusion it may be pointed out that the climax forest of the plot under consideration is the western larch-Douglas spruce formation. This association occupies a greater portion of the comparatively level stretches of Swan River valley (*fig. 8*). It also is found on the protected slopes and foothills of the low Swan Range. No attempt was made to determine its range outside of the region mapped. The trees that are characteristic of this forest are western larch, Douglas spruce, silver pine, lowland fir, Engelmann spruce, and lodgepole pine.

THE DOUGLAS SPRUCE-BULL PINE (MESO-XEROPHYTIC) AND THE PRAIRIE (XEROPHYTIC) FORMATIONS.

Since the Douglas spruce-bull pine associations and the prairie are more or less connected, they will be treated together. A reference to the map will show that a rectangular plot of ground known

as Nigger Prairie lies just north of Swan Hill, at present used for farming purposes. It is bordered on the south, east, and west by narrow strips of pure bull pine forests, and on the north a forest of

FIG. 14.—View of bull pine forest south of Echo Lake; in the center is a large bull pine, the younger growth around consists of bull pine with some Douglas spruce. —From photograph by PRAEGER.

the same species extends to Echo Lake (*fig. 14*). This bull pine stand is surrounded on all sides by a mesophytic forest in which western larch and Douglas spruce almost entirely replace bull pine.

The question arises, what is the cause of this difference in the character of the vegetation in so limited an area? So far as could be ascertained, trees have been absent from Nigger Prairie for at least twenty years, and it is very probable that it has never been forested.

The character of the soil in both the prairie and the bull pine zone surrounding it is decidedly different from that of the country immediately adjacent. That to the south and west is a residual clay from the dolomite shale of Swan Hill; that to the east is a clay rich in humus; and that to the northwest, north, and northeast is a pebbly clay of glacial origin. On the other hand, the soil of the entire prairie and bull pine region is composed of sand mixed in places with a considerable amount of humus. The limits of this sandy area extend a little beyond the limits of the bull pine forest. It seems very probable that the absence of any other trees than bull pine is due chiefly to the physical character of the soil. It must be remembered that the climate of the area under discussion is such as barely to favor a forest, and a slight difference in the amount of water which the soil can hold may lead to the exclusion of certain trees, and in places of all trees. Since a sandy soil lets water drain through it readily, it is very likely that this area is too dry to support a mesophytic forest. As shown by wells, the underground water level in Nigger Prairie is some distance below the surface, so that those trees which have shallow root systems would not be so likely to succeed as those whose root systems are extensive and deep. The bull pine is one of the latter kind, and it is very likely that this is one reason why it has the habit of growing in drier situations than some of the other trees.

If the surface layers of a sandy soil can be made to retain water, the objectionable feature of such a soil will be partly overcome, and this can be brought about by an accumulation of humus. Lower forms of vegetation, even grass, by their decay will add to the humus content of the soil. In very dry countries this accretion would be exceedingly slow, for the oxidation of the organic débris would be great; but even in dry situations by the accumulation of a slight amount of humus the water-holding capacity of the soil might be increased sufficiently to tide a few trees over the driest months of the year. Trees once established in this way would help accumulate

humus more rapidly, for by fall of the dead limbs and leaves more organic material would be added than from the decay of lower forms of vegetation. The shade of the trees thus established would check the rapid oxidation of the organic material that takes place in the open. The ultimate effect would be the establishment of a forest in a place that was formerly occupied by a prairie. It is very probable that the whole yellow pine area just described was at one time occupied by a prairie vegetation. There is evidence that the present prairie island in this forest would become covered with forest trees if not interfered with by man, for along the roadside groups of young growth of bull pine seedlings are not uncommon. All around the border of the prairie young trees are present, and even in a timothy field there were noted seedlings that had escaped being cut by the mowing machine. Before the prairie island was settled it is very probable that surface fires swept it occasionally and thus checked the conquering of the prairie by the forest. Another prairie area similar to the one just described lies directly west of Echo Lake (*map*). Again, west of Nigger Prairie, just across the low range of Mission Mountains, is another "sand pocket" that has a prairie vegetation. These however border on the prairie climate.

The question arises whether the presence of bull pine will in any way change the conditions sufficiently to make them capable of supporting other species of trees. It was shown that the humus content of the soil increases more rapidly when trees are present than when they are absent. With the gradual increment of organic decay, it is very possible that the water-holding capacity of the soil may be increased to such an extent that it will be rendered capable of supporting other species of trees.

A bull pine seedling does not tolerate shade; the young tree must have broad open places where the sun strikes the soil a greater portion of the day. An opening in the forest made by the removal of one or two trees does not allow sufficient light and heat to enter; thus young stands are excluded from anything like a tolerably thick growth of these trees. This is not the case with western larch and Douglas spruce; it has been shown that the former does not tolerate shade, but grows in slight openings in the forest; the latter is very similar in this respect to western larch. If humus has accumulated

FIG. 15.—View of an arm of Echo Lake, showing submerged cabin and timber land; a few years ago this was dry land; the trees in the foreground are western larch and Douglas spruce.

so as to give the soil a sufficient water-holding capacity, open places in the bull pine forest may permit seedlings of both the species named to thrive. Numerous instances of this were noted in the bull pine forest under consideration. In places where bull pine had been removed there were clumps of young trees of Douglas spruce and western larch. If the place is sufficiently open, bull pine seedlings are found with the others. It will be seen readily that such a condition will lead to a gradual replacement of the bull pine forest by the Douglas spruce-western larch combination. There is some evidence that such a succession has already taken place, for all around the borders of the "sandy pockets" western larch and Douglas spruce are more numerous in places than bull pine. There is also reason to believe that in the pebbly clay morainic soil around Echo Lake, especially to the south and northwest, a more or less pure bull pine stand preceded the present stand consisting of a mixture of the three species. The bull pines are found in groups, or solitary full-grown specimens overtop the younger growths of the next generation of Douglas spruce and western larch, these isolated specimens doubtless representing all that is left of the former pure bull pine stand. Of course this succession has been a gradual one, occupying many generations, the more successful trees elbowing their way, as it were, among the less successful until the spread of the latter is limited by their incapacity to adapt themselves to the new environment. All stages in this succession are present today in the forest under discussion, and it was the study of these stages that led to the conclusion that has been advanced.

Out towards Flathead River the zone between the prairie and the forest contains a few scattered specimens of bull pine; next to this there is a more dense stand of this species with a few scattered trees of Douglas spruce; back farther still from the prairie is a zone in which bull pine is less and Douglas spruce more frequent; and finally another condition is found in which western larch joins these two species, bull pine being the least conspicuous element of the three. Such an arrangement is approximated just west of Echo Lake. This region is decidedly morainic in its character, and where depressions approach the underground water level western larch becomes more numerous, and in places near Echo Lake the surface

of these depressions comes near enough to the water level to permit the growth of scattered Engelmann spruce. This level of underground water varies, and this change is shown in the rise of the lake itself and the ponds around it (*fig. 15*).

Mention has already been made of the western larch-Douglas spruce combinations on the protected slopes of the Mission Moun-

FIG. 16.—View on the top of the Mission Mountains showing area on which the Douglas spruce-bull pine forest has been destroyed by fire; the outcrop of dolomitic shale has been scoured smooth by the action of glacial ice; Ceanothus bushes on the right, lichens of various sorts on the rocks, and prairie grasses where the soil is sufficiently deep.—From photograph by PRAEGER.

tains. Toward the top of this slope western larch becomes less and Douglas spruce more prominent; in places the latter is mixed with lodgepole pine. On the west side of the range Douglas spruce and bull pine are the principal species; hence this area has been mapped as meso-xerophytic, although western larch is present in some situations.

The altitude of the Mission Range within the limits of the plot is nowhere more than 1372^{m} above the level of the surrounding country. The core of the mountains is composed of a dolomite shale, which outcrops in many places. Especially is the rock near the surface on the steep northwest fault face and where the soil has been removed by the action of glaciers (*fig. 16*). South of the river the forest on the western slope has been partially destroyed by fire (*figs. 16* and *17*), but enough of the original stand remains to give a clue to the conditions of the whole slope. A discussion of the burned area will be taken up in another connection.

Wherever the rock outcrops there is little or no vegetation (*fig. 16*), due to the fact that there is no soil; the pioneer plants on the rocks here, as elsewhere, are the lichens. The crustaceous lichens appear where there is absolutely no disintegrated rock; sometimes associated with these are the foliaceous forms, but these are more common where a little soil has accumulated; with these are found mosses adapted to the dry conditions. After more soil has accumulated, conditions are favorable for plants that require more moisture; among these are the fruitcose lichens, *Cladonia rangiferina sylvatica* being a good example. Associated with these lichens are *Selaginella densa*, *Sedum Douglasii*, *Heuchera parvifolia*, the last being usually found rooted in cracks. These plants prepare the way by their decay for the higher forms that can get a foothold as soon as sufficient soil is present. The inorganic material made by the disintegration of the rocks is blown or washed in from the surrounding region and reinforces the organic accretion. In the meantime the rock crevices have been filling up with soil, thus furnishing favorable places for shrubs like *Prunus demissa*, *Symphoricarpos* sp., *Amelanchier alnifolia*, and *Juniperus sibirica;* and *Campanula rotundifolia*, *Arctostaphylos Uva-ursi*, and grasses are early pioneers in these places. If the outcrop is near a large body of water like Flathead Lake, *Juniperus scopulorum* is one of the first trees. This tree is found distributed around the shores of the lake and along water courses in the prairie region in the valley at the foot of the lake, and with it are found Douglas spruce and bull pine. These of course gain a foothold by sending their roots into the rock crevices and may play an important rôle in the weathering processes by prying the rocks

FIG. 17.—View of burned region on west slope of Mission Mountains; Daphnia pond nearly filled with hydrophytic vegetation; the forests of larch, Douglas spruce and bull pine almost entirely destroyed; the bushy growth that becomes vigorous after the forests have been destroyed is Ceanothus, Amelanchier, Salix, etc.—From photograph by ELROD.

apart in the growth of their roots. However, on the rocks there is never more than a scattered growth of trees. Where the soil is less shallow, more trees are present and a more closed stand is developed. In the ravines and other situations where a deep soil has accumulated, a heavy growth often occurs; especially is this true in the protected ravines and on the sheltered slopes. Along the front of Flathead Lake there is a series of ridges which has an open growth of Douglas spruce and bull pine on the side facing the lake; and protected from winds, the slopes on the east side of these ridges and the valley between them and the higher ridges to the east have in addition western larch, which in places is the dominant tree. Again, where the surface of this valley is not far above water level, Engelmann spruce and its associates are found, though these places are infrequent. In many protected areas on the west side of the Mission Range western larch is present, though as contrasted with the eastern slope the exposed western face of the mountains is not so favorable a habitat for the mesophytic trees.

The temperature conditions on top of these mountains and at the foot are not known. No doubt the climate is considerably cooler at an altitude of 1372^{m}, the highest point of the range in the plot, than it is at 890^{m}, the level of the lake. However, this difference is not enough to exclude the lowland species and introduce those found on the higher Swan Mountains to the east. The presence of a large body of water like Flathead Lake no doubt influences the temperature conditions along its shores, for early fall frosts are less frequent here than at a short distance inland. Whether or not this affects the forest growth is not known.

THE FORESTS OF THE FLATHEAD VALLEY, MONTANA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXVII.

HARRY N. WHITFORD.

(WITH MAP AND TWENTY-THREE FIGURES)

[*Concluded from p. 218*]

THE undergrowth of the Douglas spruce-bull pine combination is decidedly heath- or prairie-like. In the more open places grass is predominant, and associated with the grasses are *Balsamorrhiza sagittata*, *Monarda scabra*, *Lupinus ornatus*, and *Clarkia pulchella*. The most common bushes are *Prunus demissa*, *Amelanchier alnifolia*, *Opulaster pauciflorus*, and *Symphoricarpos* sp. In places where the rock is near the surface a heath-like appearance is given to the undergrowth by the presence of *Cladonia* sp., *Arctostaphylos Uva-ursi*, *Campanula rotundifolia*, *Selaginella densa*, *Lepargyraea argentea*, and *Pteridium aquilinum;* other forms noted were *Galium boreale*, *Achillea millefolium*, *Holodiscus ariaefolia*, and *Populus tremuloides;* and along the pebbly shores of the lake Crataegus is very characteristic.

On the southern slope of Swan Hill the vegetation conditions found on the exposed slopes of Mission Mountains are approximated, though this area is slightly more mesophytic; and the same may be said for the east side of Swan Lake. Here the shores end abruptly in a range of hills on whose west slope Douglas spruce and bull pine are characteristic, though here and there are scattered groups of western larch. Another meso-xerophytic area on the east side of Big Fork River, not far from the foot of the lake (*map*), has already been mentioned.

The country lying to the south and southwest of Flathead Lake is semi-arid (*fig. 5*), but in favorable situations there is some woody vegetation. A fringe of trees around the borders of the lake contains principally Rocky Mountain juniper, hawthorn, and bull pine; and the same condition is found along Pend d'Oreille River where

a low terrace has been formed. Dry ravines extending back from this lake also have a woody vegetation. The difficulties which trees meet in getting a start in a prairie region should be recognized. A very large majority of the seeds never germinate, and many that do germinate dry out before they have made a good start; and the sod also in many instances prevents the seeds from reaching the soil. The head of a ravine works back during freshets, undermines the prairie sod, and thus disturbs the vegetative equilibrium that had been established, offering a place more or less free from competition. If seeds fall on one of these bare places and do not dry out before the next rain which disturbs more of the soil, they may be buried by the moving soil; the seeds thus having the advantage of being planted and supplied with moisture at the same time. If the conditions remain stable long enough for the plant thus started to establish itself, it may hold its own even though there is considerable movement of the soil in the erosive process. Of course only a few plants out of the number thus established can exist long in the severe conditions of drouth that prevail in these regions.

The large moraine at the foot of the lake is almost destitute of trees (*fig. 5*), but isolated trees of Douglas spruce and bull pine were observed on its northern slope, and around them were a large number of seedlings, nearly all of which, in spite of their needle-like leaves, were nipped off by the cattle. It is very possible that if it were not for the cattle more of the trees would reach maturity, though it is doubtful if the increase would be very appreciable. However, if a slope was slightly more protected from the drying winds and the cattle did not interfere, open stands of both Douglas spruce and bull pine might exist. The hillside near the region shown in *fig. 6* illustrates the point; it slopes to the north, and the part of it under discussion is too high up the cañon of the Pend d'Oreille River to be influenced by proximity to the river, though probably trees near the river are the source of supply for the seeds that stocked the hillsides higher up. The bank is too steep for cattle to maintain a foothold easily, and except along paths young trees are not eaten by them.

As one approaches the forest formation to the north and east from the south end of Flathead Lake, trees become more prevalent, a number of hilly islands (*fig. 5*) in the lake showing an interesting

series of gradations. First there are hills with bull pine and a few Douglas spruce on the north and east slopes and few or none on the exposed slopes; then there are hills where a considerable number of bull pines find favorable conditions for development on the exposed sides of the hill (*fig. 18*), and with these there is some Douglas spruce. On the protected slopes the Douglas spruce becomes more abundant and may even destroy new growths of bull pine by their shade. Another set of hills nearer the forest formations show the south slopes fairly well covered with bull pine and Douglas spruce, while the bull pine has become less abundant on the protected slopes where the western larch element has been introduced. Thus there are all gradations from hills with few or no trees to those that have mesophytic elements on the north slopes. Of course there are many variations; for instance, hills a little to the north of west of the town of Big Fork have their southern slopes almost destitute of trees, while the protected slopes have a stand of Douglas spruce, western larch, and some bull pines. The series may be carried still further. It has been shown that the west slope of Mission Mountains has a forest of Douglas spruce and bull pine, while on the protected slope western larch is the most prevalent, and with it trees like lowland fir, silver pine, and giant arborvitae, which require still more moisture, are found. If the rainfall be sufficient, a mesophytic forest may be found on the exposed as well as on the protected slopes.

It may be well to analyze the conditions that make the so-called protected slopes more desirable for trees. Of course the great factor that prevents tree growth is the lack of moisture. If an annual rainfall of 400^{mm} falls upon a hill similar to those just described, and in gentle showers so that there will be little or no run-off, the water that leaves the soil directly must do so by evaporation, the remainder soaking in and becoming available for absorption. It is obvious that the slopes receiving the strongest insolation and exposed to drying winds will lose the most water by evaporation, and these are the south and west slopes; hence the north and east slopes will have more moisture in the soil. Again, the plants growing on these protected slopes do not receive so much heat and are not exposed to the drying winds, hence do not lose so much water by transpiration; they not only get more moisture but do not need so much to supply

the transpiration streams, therefore trees that require better moisture conditions can exist in these situations.

The sylvicultural habits of Douglas spruce and bull pine remain to be summarized. Douglas spruce has the widest life range of any of the species found in Flathead valley, being found at higher altitudes than any other of the lowland species, with the exception of

FIG. 18.—View of a portion of an island near the south end of Flathead Lake; a park-like growth of bull pine and Douglas spruce is present.

Engelmann spruce. It is found accompanying western larch all through the mesophytic forests of Swan valley, and forms even a greater percentage of the trees in the meso-xerophytic regions, and advances into the prairie sometimes as far as bull pine. However, this power of adaptation is not without an effect upon its form, for in high altitudes and on the border of the prairie region it is dwarfed and sometimes fasciated. In mesophytic conditions it reaches the dimensions of the trees with which it is associated, and even these

trees, though larger than most of the conifers of the eastern states, are small compared with the vigorous trees found in the hemlock-arborvitae-Douglas spruce forests west of the Cascade Mountains. It is in this region of greater rainfall and warmer winter months that Douglas spruce makes its best growth. With its great power of adapting itself to adverse conditions, it has spread through all the Rocky Mountain region as far south as Mexico. While Douglas spruce can adapt itself to varying conditions of moisture, it is very intolerant of shade, in this respect being like western larch, and even requiring slightly more open places in the forest to gain a foothold. Thus the tree will be reproduced only in open places in the forest.

The distribution of bull pine in Flathead valley is more limited than that of either Douglas spruce or western larch. It occurs in open park-like growths on the borders of the prairie formation, with patches of the prairie between (*fig. 18*). In the forest formations in the vicinity of Nigger Prairie there is a close stand of this species (*fig. 14*). Indeed so thick are the trees in certain situations that there is not sufficient light under them for the reproduction of either Douglas spruce or western larch, though young trees of Engelmann spruce and lowland fir can endure the shade. Isolated groups of bull pine are scattered through Swan valley, usually along streams where abundant light can reach them, and in pebbly soils, where other trees have difficulty in maintaining a stand, bull pine is found. Wherever a single tree is found surrounded by other trees it usually overtops them, showing that it probably started before they were present, for it is exceedingly intolerant of shade; it must have open places in which to pass its young stages, and this perhaps accounts for its scarcity in the mesophytic area in deep rich soils. Where found in Swan valley, it is a very healthy tree and very likely would do well in pure stands there if given a chance. In other words, bull pine does not grow in the dry soils on the border of the prairie because it prefers the moisture conditions found there, for it does better in the soils where there is more moisture; it is almost entirely forced out of the latter soils in the struggle for existence with the more successful trees. It undoubtedly demands a greater amount of heat than the other species, with the possible exception of lowland fir, for its altitudinal range is more limited. The highest point at which it was observed on the surrounding mountains was 1375^{m}.

A summary of the relation of the prairie to the forest in this region is as follows: (1) there is less moisture in the prairie soil than in the forest soil; (2) this is due primarily to the smaller amount of rainfall; (3) in the prairie formation forests may exist in certain topographic situations, as along streams and other bodies of water, and on protected hill-sides; (4) in the forest formation prairies exist where the character of the soil is such that it will not easily hold water; by the gradual addition of humus such soils may be changed sufficiently in their water-holding capacity to permit more mesophytic conditions and in some instances a climax western larch-Douglas spruce combination.

Objection may be made to the use of the term mesophyte for plants with xerophytic leaves. WARMING classifies all conifers as xerophytes because they grow in dry soils. In the eastern United States in contrast with the broad-leaved deciduous trees the conifers are undoubtedly xerophytes, comparatively speaking. That is, during the summer months the deciduous tree requires more moisture than the conifers, therefore the deciduous tree is excluded from the dry soils. In the northwestern United States the coniferous forests occupy the mesophytic soils almost to the entire exclusion of the deciduous element. As shown in the discussion on the climatic formations, this is due to a peculiar climate in which the summers are comparatively cool and dry, and the winters comparatively warm and excessively wet. In such a climate the deciduous tree is lacking, except in edaphic situations, on account of the cool dry summers, because with its broad transpiring surface it requires more moisture than it is able to get. The narrow-leaved sclerophyllous trees, on the other hand, while they do not necessarily thrive during the dry summer months, because of their reduced transpiring surface they are permitted to exist, while the broad-leaved deciduous trees cannot. During the winter the reverse is the case, for deciduous trees with their bare twigs are better able to endure severe conditions than are the conifers. On the other hand, if the climate is moist and warm, the conifer is able to do a considerable amount of photosynthetic work. Thus the deciduous tree requires more moisture during the summer months and is consequently more mesophytic at that season; on the other hand, the coniferous tree requires more moisture during the winter months and consequently is more mesophytic at that

time than the deciduous tree. Because of the equable distribution of moisture throughout the year in sufficient quantity in the eastern United States both can exist, although the deciduous element is able to occupy the mesophytic areas almost to exclusion of the coniferous element. In the northwestern United States the conifers, because the climate in which they grow is more suited to them, are able to occupy the mesophytic areas, and hence, so far as that climate is concerned, are mesophytes. Although they may have xerophytic leaves, the structure of the tree as a whole is more mesophytic during the non-growing season than is that of the deciduous tree. Taking the entire year into consideration, for the reasons given above I think that I am entirely justified in speaking of conifers as mesophytes.

III. The influence of fires on the present composition of the forests of Flathead valley.

In the discussion of the forest conditions up to this point little attention has been given to the influence of fires. There is scarcely a section of land in the area investigated that has not been more or less burned over. In some places mere surface fires have run through the woods, scorching the trunks of the trees sufficiently to scar them. In other situations the fires have burned vigorously through small areas killing many of the trees. Still other fires have destroyed completely large areas, leaving many acres with not a single tree. Such is the case on the west slope of the Mission Mountains (*figs. 4, 16, 17*). There are many small clearings made by settlers, who after proving up their claims have deserted the cabins erected upon them (*fig. 19*).

By marshaling the facts collected by a study of the conditions of reforestation in these fire clearings, nearly all stages in the establishment of new mature forests were determined. Studies in similar regions outside of the area plotted have proved very helpful in the interpretation of these conditions. Some important principles must be kept in mind in explaining what plants will first get a foothold in the open places made by fires. These are as follows:

1. The subterranean parts of some plants that are able to sprout from roots or underground stems may not be destroyed by fire. The sprouts of these species will give the burn a decided aspect in a short time.

2. Other things being equal, the plants whose seeds are in the burn first will gain the earliest foothold.

3. Those plants that have seeds there early after fires will be those that have seeds well adapted for distribution.

4. Of the plants that have their seeds equally well adapted for distribution, those with seed-bearing representatives standing nearest the burned area will have the advantage.

5. Again, other things being equal, of those species that have their seeds equally well adapted for distribution and have seed-bearers equally near the clearing, the species that produce seeds most abundantly will be apt to win out in the struggle.

6. The species that can resist fires the best are likely to have left standing in or near the area itself seed-bearing parent plants.

7. The conditions of the soil must be such that it will permit the germination of the seeds that fall upon it. If the soil is too moist, too dry, too poor, or too much shaded, no matter how many seeds fall upon it, none will germinate.

These well-known principles will aid in the determination of the causes of the many complex conditions of forest growth after fires. Before the actual conditions of the clearings are considered, however, the ecological habits of another tree, the lodgepole pine, must be known.

The lodgepole pine covers large areas in Swan valley, sometimes forming almost pure stands. It is able to exist and thrive in those moist areas where it has to compete only with the spruce and its associates. It is found mixed with all the other species in the mesophytic portion of the valley. Toward the borders of the meso-xerophytic areas it is not so prevalent, though signs of it were noted west of Echo Lake and in the mesophytic portions of the west slope of the Mission Range. It does not advance into the prairie formation, however, so far as the bull pine and the Douglas spruce. Its altitudinal range was not investigated. It is difficult to tell whether or not this tree would maintain a stand in the Flathead valley if it were not for the influence of fires. It is intolerant of shade, in which respect it may be ranked with western larch and Douglas spruce, reproducing in open places only. No young trees were noted in the shade, save an isolated poorly developed specimen now and then

in the slight shade of a mature stand of the same species. Probably it is a little less exacting in its light requirements than western larch and Douglas spruce.

The lodgepole pine is a prolific seeder, beginning to bear fruit early in life. Out of twenty trees varying in age from five to twenty years, many had cones. The youngest tree noted with cones was six years of age, one at this age having seven cones. On one tree nine years old fifty cones were counted. It was a common thing to find clumps of trees 3 to 4^{m} high fruiting abundantly. As will be shown below, this habit of fruiting early in life is of very great advantage to this species. Another thing of very great importance is the fact that the cones remain closed in some instances a number of years, thus preserving the seeds. The heat of a fire will open them and liberate the seeds, many of which will escape injury and germinate at once. The lodgepole pine, during its early stages at least, grows rapidly in height, and this gives it some advantage over its competitors. From the measurements of twenty-five specimens each of lodgepole pine, western larch, and Douglas spruce, the average rapidity of growth in height per year is shown to be as follows: lodgepole pine 52^{cm}, western larch 27^{cm}, Douglas spruce 20^{cm}. Although these averages are from rather meager data, they are sufficient to show that the lodgepole pine has by far the most rapid growth.

In contrast with western larch, Douglas spruce, and bull pine, lodgepole pine has poor fire-resisting qualities. Except in old trees the bark at the base is comparatively thin; the cambium layer is thus easily scorched and killed. In this way many whole forests of trees are destroyed by fires that are not intense enough to consume the trunks. It is not an uncommon thing to see acres of dead standing poles of this species that have thus been swept by fire. In showing how successful lodgepole pine has been in obtaining a foothold in the forests of Swan valley, the principles mentioned above must be kept in mind. The rôle that the plants other than conifers play in the reforestation stages will be treated in another connection. In order that the conditions may be understood more clearly, hypothetical cases will be assumed, and when these hypothetical cases are realized attention will be called to them. Suppose a limited area is burned in the midst of a forest in which western larch and Douglas

spruce are the dominating trees, and that these are mixed with lodgepole pine, silver pine, and lowland fir. Suppose that the trees surrounding this area all bear cones, and all have their seeds equally well adapted for wind distribution. Since not one of the conifers found in the region is able to sprout from the roots that would be protected from the fires, all would have to start from seed. Let us suppose

FIG. 19.—A clearing in a lodgepole pine forest in Swan valley; east slopes of Mission Mountains in the background; these slopes have a mesophytic forest of western larch and Douglas spruce.—Photograph by PRAEGER.

that the seeds of all fall in equally favorable places, and that the seedlings that spring up are numerically proportional to the parent trees in the undestroyed stand surrounding the burn. Each species in the forest adjoining the new growth will thus be represented in the burn in the same proportion as it is in the mature stand. If all the young trees grow with equal rapidity, and the natural thinning out is proportionately distributed among the species, the new stand will be just like the old. There are some small burns where this

condition is approximated; of course the proportions are not exactly the same in the old and new stands (*fig. 20*). Granted that any one of the species in the young forest grows more rapidly in its youth than the others, other things being equal it would gain an ascendancy over its neighbors, and in the forest approaching maturity it would have more representatives than in the old forest. As already shown, lodgepole pine bears exactly that relation to Douglas spruce and

FIG. 20.—Young growth of lodgepole pine and western larch in a clearing surrounded by older trees of the same species, both of which have seed-bearing trees; other plants are dwarf maple and a willow, both of which sprout from old stumps; fireweed is also a characteristic plant.—Photograph by PRAEGER.

western larch at least, and probably to the other species, though no measurements were taken for them. In the new forest thus established, lodgepole pine has made a gain on the other species. However, it reaches maturity sooner than the others, and in the old forest it is the first to drop out in the struggle for existence, so that while in the middle-aged forest it may have had some slight advantage, it loses this and often is entirely eliminated from the mature stand.

Many instances were noted, especially in the region outside the plot mapped, in which lodgepole pine was thus being driven out of forests where doubtless it was more prominent in the young stages of development.

Referring again to the original case, it will be seen to be highly improbable that the species in the stand around the hypothetical burn

FIG. 21.—Young growth of lodgepole pine and Engelmann spruce in a clearing of the same species.—Photograph by PRAEGER.

would produce seeds equally well. Some species might not have any seeds at all, and they would form no part in the new forest unless a few seeds are blown into the area from regions where there are seed-bearing trees. The lowland fir during the past two years has produced few if any seeds in Swan River valley. Any burn made in the valley then within two years could not be stocked with seeds of this species. If for instance Douglas spruce or western larch produce seeds more abundantly than any of the other trees, they are likely, other things being equal, to have more representatives in the

new forest than in the old. So if any other tree, lodgepole pine for example, has more seeds than the others, it will increase in numbers in the new stand that is formed. So far as its relation to restocking a burn is concerned, a tree that does not produce seeds might just as well not exist at all.

This leads naturally to another modification of the hypothetical case, in which the forests that surround the burn have only one or two species instead of a number. The result will be that these species are likely to be the only ones found in the burn. Such a condition is seen in *fig. 20*, where the forest that surrounds the clearing is composed mostly of western larch and lodgepole pine, and these species are the predominating ones in the new growth. *Fig. 21* shows a clearing surrounded principally by lodgepole pine and Engelmann spruce, which are almost the only trees present in the new stand. Again, *fig. 22* shows that bull pine, western larch, and Douglas spruce are present in an opening in a mature forest of these species. Another explanation for this, however, is that the area is situated on the border of the meso-xerophytic region where probably no other species could exist, even if their seeds were present.

This leads to still another modification of the hypothetical case. Assuming that the seeds of all the species are present, it is highly improbable that they would find equally favorable places for germination. The case just cited (*fig. 22*) is an instance of where all except western larch, Douglas spruce, and bull pine are ruled out. If the fire burnt out an Engelmann spruce stand surrounded by a less swampy region in which Engelmann spruce, lowland fir, silver pine, Douglas spruce, western larch, and lodgepole pine were present, only Engelmann spruce and lodgepole pine would be able to restock it, for these are the only species that could grow in the swampy situations. An instance of such restocking was noted near the head of the bay-like area of meso-hydrophytic forest southwest of Ross Lake.

Still other conditions of reforestation remain to be explained. Taking the hypothetical area that has been restocked with the seedlings of all the trees in the surrounding forest, and assuming that the young growth is approximately fifteen years of age, the only species of this young growth that would have fruit is lodgepole pine. The cones on this pine would be more or less abundant, and on all

the others the cones would be absent. If a fire should sweep through this young growth, destroy it, and at the same time consume some of the original forest around it, thus extending the limits of the original burn, what would be the result? The extent of the burned area being greater, the seeds of the trees bordering it could not so readily be carried to the center of the burn. But this portion of the clearing would be restocked with the seeds of young lodgepole pines that were destroyed by fire, but whose seeds would be more or less protected from the fire by the cones. Some of the cones would be cracked open by the heat of the fire and the seeds would be liberated. The result would be that the next forest would contain more representatives of lodgepole pine than the former forest, and that they would be more numerous in the center. Indeed this center might contain a pure growth of lodgepole pines. Another such fire in the course of fifteen or twenty years or less would enlarge this area at the expense of the other species. Thus almost if not quite pure forests of lodgepole pines of considerable extent would be established. It is very probable that the mature lodgepole pine forest found in Swan River valley was established in this way (*fig. 23*). The evidence for this is as follows:

1. In no case was a stand of this species found in which there were not noted dead and charred trunks of western larch and Douglas spruce, mostly the former; these because of the thick bark would be the last to yield to the fire. In some instances mature live trees of western larch were observed towering above the younger lodgepole pine forest. In these cases there were isolated specimens of young western larch of about equal age growing with lodgepole pines (*fig. 12*).

2. In nearly all cases these forests grade imperceptibly into more mature forests in which the lodgepole pine element is entirely or nearly wanting. The mature forests of western larch, Douglas spruce, silver pine, lowland fir, and lodgepole pine are in many instances growing in soil that is similar in moisture content. Thus it cannot be said that the difference in the two stands is due to the character of soil conditions.

3. In the meso-hydrophytic situations there is often a gradation from a spruce forest to a mixture of Engelmann spruce and lodgepole pine, the latter stand being much younger than the former.

4. In stands that contain little or no signs of fires, the lodgepole pine element is absent or nearly so.

5. Nearly all stages in the development toward this condition were noted. Thus, *fig. 20* shows a comparatively recent clearing in a young lodgepole pine forest, which is in turn surrounded by a mature forest of western larch and Douglas spruce in which the lodgepole pine element is inconspicuous. *Fig. 12* shows an almost pure growth of this young forest with mature trees of western larch in it. In another place there is a more mature growth in which only charred trunks of larch tell the tale.

For the reasons given above, it is believed that the explanation for the lodgepole pine in the area plotted is the correct one. As before stated, observations were not limited to this immediate region, and many instances might be cited where burned areas similar to those described have become reforested with lodgepole pine. It will not be out of place to repeat that the advantage which it has over the other species in the region is due to its capacity to produce seeds early in life, and its habit of retaining the seeds in its cones for a number of years, thus preserving them for a greater or less length of time. In forests partially destroyed by fire the trees of western larch and Douglas spruce, because of the capacity of their trunks to resist rather severe burnings, will restock the burned areas. Fires of this nature, repeated sufficiently often to prevent any young lodgepoles from becoming old enough to produce cones, will militate against the latter, while Douglas spruce and western larch will have cone-bearing trees on the ground so long as the fires are not too intense. As soon as these are destroyed, then the seed supply is cut off and restocking from that source at least will discontinue.

It will be seen readily that if the fires that have made the lodgepole pine condition possible are repeated every five years, for instance, the young growth forests of that tree will not be permitted to follow each other in procession, for the five-year interval between fires will be too short a time to permit lodgepole pine to produce seeds. Then of course all forest growth will be completely destroyed and the area will not become clothed with trees until restocked with seeds from the neighboring undestroyed forests. The further these are away, the longer it will take for seeds to reach the devastated area. However,

if the interval between the fires is sufficiently long to give lodgepole pine time to produce seeds, after each fire a forest of lodgepole pines will spring up to replace the old. Such fires enable lodgepole pine to perpetuate itself so long as the soil is able to furnish the requisite amount of nourishment, but a checking of fires will in time bring about the normal conditions. This has been done about as follows:

The fires being absent, the lodgepole pine stand is permitted to reach maturity. As it does so, seeds of forest trees in the neighboring undestroyed or partially destroyed stands have had time to spread into the lodgepole pine forests. Seedlings of those trees that can tolerate the shade will get a start at once, if the other conditions are favorable. Thus in many instances silver pine, lowland fir, and Engelmann spruce were noted growing under lodgepole pine stands in Swan valley. Also in the Terry Lake region seedlings of giant arborvitae and western hemlock were observed in similar situations, although, because of the restricted area to which

FIG. 22.—Young growth of western larch, Douglas spruce, and bull pine in a clearing of the same species.—Photograph by PRAEGER.

these two species are confined, their occurrence under lodgepole pine stands is not common. As soon as openings are made in the forest of mature lodgepole pines, due to causes other than fires, this undergrowth may spring at once into prominence and may come to occupy a place in the mature forests. At the same time the openings have made it possible for the existence of seedlings of such trees as western larch and Douglas spruce which demand light for germination. Of course lodgepole pine seedlings can germinate here also, and in the first generation or two they will still predominate; but each new generation will have fewer specimens of the latter species, for since it is not a long-lived tree, a canopy of the mature forest of the other species will in the long run crowd it out by density of shade, or reduce its occurrence to isolated trees here and there in the forests. In this way the forests will revert to the normal conditions. The time it will take to do this depends upon the nature of the conditions that the last fire left. If the lodgepole pine conditions had been established for a wide area, the time would be long, perhaps covering many generations of growth. If on the other hand the fire only partially destroyed the original forest, one or a few generations would suffice to permit the re-establishment of a forest similar to the original. Between these two extremes are all stages, some of which have been described. Indeed the present forest formations are a complex expression of the influence of fires upon them.

The general aspect of a lodgepole pine forest approaching maturity is somewhat different from that of other stands. It has already been shown that the growth in height is rapid. In dense stands of young growth the poles are long and spindling, hence the name lodgepole pine. The small diameter of the bole of the tree is very characteristic. A forest in which the average age of the trees is about one hundred years is seen in *fig. 23*. In this forest, where the trees are over a hundred years old, the average diameter is probably 20^{cm}, many trees being only 15^{cm} in diameter.

Compared with the other forests growing in like situations, the canopy that a lodgepole forest forms is not very heavy. This permits more light to reach the forest floor, hence there is a greater development of undergrowth. It has already been shown that seedlings of silver pine, Engelmann spruce, and lowland fir can endure

the shade of these forests, and that except in open places Douglas spruce, western larch, bull pine, and lodgepole pine are ruled out altogether. The birch is found scattered throughout the limits of the forest. Indeed, as will be shown, it is often a conspicuous tree

FIG. 23.—Mature lodgepole pine forest in Swan valley, showing a dense stand in which the trunks are 15 to 20^{cm} in diameter; the undergrowth consists of *Acer glabrum*, Pyrola, Pteridium, Linnaea, etc.—Photograph by MCCALLUM.

in the burns, and grows up with lodgepole pines, though as the forest matures it drops out early. The undergrowth consists of *Acer glabrum*, *Lepargyraea canadensis*, *Symphoricarpos* sp., *Rosa* sp., *Lycopodium* sp., *Pyrola secunda*, *Pteridium aquilinum*, *Linnaea borealis*, *Chimaphila umbellata*, *Clintonia borealis*, and *Aralia nudi-*

caulis. Scattered specimens of juniper are found in places. In other respects the forest is like the other stands in the mesophytic regions.

In what has been said concerning fires, no mention has been made of species other than conifers. They may often play an important rôle in the first stages in the natural process of reforestation, but their importance diminishes as the life history becomes complete. One of the first plants to give a decided aspect to the forest after fires is the fireweed (*Chamaenerion angustifolium*). The birch and aspen, by virtue of their light seeds, gain an early place in the burns. Indeed sometimes their stands become quite dense and they check the advent of coniferous species. Many species that were on the forest floor of the mature stand may have survived the fires and spring up even more vigorously than before, because the shade has been removed. Especially is this true of those forms that can send shoots from their roots or from underground stems. In the burn on the east slope of the Mission Range south of Big Fork, there are shrubby growths of *Salix* spp., *Ceanothus sanguineus*, *Opulaster pauciflorus*, *Acer glabrum*, and *Holodiscus ariaefolia*, many of which probably were present as underbrush in the stand that existed previous to the burn. These shrubs will retard the reforestation of the area in some instances to a marked degree. If the forest that is destroyed be on the border of the prairie, plants from that association will form an important element in the growth that follows. This is of course detrimental to forest growth. Indeed if the fires be repeated often enough, the forest plants will gradually diminish in quantity, and the prairie element will become more and more prominent, until finally a prairie will come to replace a forest. If the fires be checked, however, for any length of time, the forest will gradually reconquer the territory thus lost. It is probable that some of the prairie region in Flathead valley has been won from the forest in this manner. It must be remembered that in the area bordering on the prairie, in Flathead valley at least, lodgepole pine is not successful and is thus ruled out from playing any important rôle in these places after fires.

In the discussion of the causes for the Nigger Prairie region, mention was made of the importance of the accumulation of humus in rendering the sandy soil more capable of holding moisture. It

can be seen that fires will tend to reduce the humus content of the soil. This is of extreme importance, for that which would otherwise add to the richness of the soil and increase its water-holding capacity is destroyed. Especially is it of importance in those regions that border on the prairie. There is evidence of many such surface fires in the open woods around Nigger Prairie, and it is very probable that these fires have played an important rôle in keeping the prairie vegetation from being encroached upon by the forests that surround it. Even in the mesophytic conditions, fires influence the capacity of the soil to reforest itself quickly, by partially or totally destroying the humus. However, with the reclothing of the burned area, the floor of the new forest will gradually resume its normal condition.

From the above it will be seen that forest fires play an important part in determining the composition of the forest. That forest fires prevailed in this region before the advent of civilized man is a logical inference. In the lodgepole pine forest in the Swan River there are unmistakable signs of fires before the present forest, which is now about one hundred years old, was started. How these fires started can only be conjectured, and it is not within the province of this paper to discuss their origin. It is also very evident that the fires are more numerous since the settling of the country by civilized man than before.

SUMMARY.

1. Fires play an important part in determining the present composition of the forest.

2. The lodgepole pine is the "fire tree" of the region.

3. It is favored after fires principally because it has the capacity to produce seeds early in its life.

4. Many complex conditions of growth are introduced after fire. The species that have seed-bearing trees near the burn will generally be represented in the new forest.

5. Repeated burnings at intervals of ten to thirty years will establish a lodgepole pine forest where formerly there existed a normal mesophytic forest.

6. Repeated burnings at intervals of five years or less will destroy all forest growth.

7. After the lodgepole forest is once established and the fires are checked, it will slowly be replaced by the species that exist in the normal forests.

8. The lodgepole pine is not successful in the bull pine belt.

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